Use of demersal bycatch data to determine the distribution of soft-bottom assemblages off the West and South Coasts of South Africa

Louise Lange

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Department of Zoology

University of Cape Town

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Declaration

I hereby declare that all the work presented in this thesis is my own, except where otherwise stated in the text. This thesis has not been submitted in whole or in part for a degree at any other university.

Signed by candidate
Signature removed

Louise Lange

27/01/2012

Date

This thesis is dedicated to my parents, Meyer and Hannie, for always believing in me and who, without fail, kept me going.

“A dredging (in this case trawling) ship may be compared with an air-ship towing a dredge (or trawl) over Copenhagen, catching a policeman in one street and a perambulator in another: and from these it draws conclusions as to the whole population of the town.”

Even Petersen (1913)

Table of Contents

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Abstract

Use of benthic bycatch data to determine the distribution of soft-bottom assemblages off the West and South Coasts of South Africa

The continental shelf surrounding South Africa is dominated by unconsolidated sediments, with scattered rocky outcrops. Our knowledge of benthic invertebrate biodiversity and distribution patterns over the continental shelf is poor and this is hampering efforts to establish a network of Marine Protected Areas that will adequately conserve the regional benthic biota. This project aims to analyse information on invertebrate biodiversity patterns of the offshore benthos around South Africa. Samples were collected as bycatch from demersal trawl surveys conducted along the South (one cruise) and West Coasts (two cruises). A pseudo-random sampling technique was employed for two cruises carried out aboard the *F.R.S. Africana*, and a structured, depth-stratified sampling technique was employed for one cruise conducted aboard the *R/V Dr Fridtjof Nansen*.

Over 250 trawls were examined, ranging in depths from 30 - 700 m. Invertebrates were sorted to species level, where possible, photographed, weighed and preserved in ethanol or formalin for later identification in the laboratory.

Invertebrate abundance and biomass data collected from both the Africana and Nansen cruises were statistically analysed using MINITAB 16.1. Groups/communities were identified using cluster analysis on the data, which were then imported into ArcGIS 9, a Geographic Information System (GIS) software program. Biogeographic and diversity patterns were then determined at a fine scale. Species diversity from abundance data were examined using diversity indices.

The results for the Nansen survey showed that Crustacea and Echinodermata were the dominant groups on the West Coast, with abundance being highest in the 200-299 m depth zone, and biomass in the 100-199 m depth zone. The Africana survey results also showed that Porifera and Crustacea dominated the West Coast, while Crustacea and Echinodermata were the prominent groups on the South Coast. Overall, biomass was highest in the 100-199 m depth zone and abundance in the 100-199 m depth zone.

Based on the benthic invertebrate samples collected during the three cruises 22 groups/communities were identified. The Africana survey revealed five groups on the West Coast, three groups on the South Coast and eight groups covering both Coasts. The Nansen survey produced six groups. Depth was the major factor determining benthic distribution patterns, with coast (location) being the limiting environmental parameter. Groups/communities locations for both cruises were assessed and the numbers of species found in each were compared. A series of offshore MPA's which take into consideration existing terrestrial reserves, were selected to conserve as many groups/communities as possible.

List of Figures

Chapter 4: Using a large-scale biodiversity data set to quantify and interpret key patterns in benthic diversity

Chapter 5: Synthesis

List of Tables

Chapter 1

BACKGROUND AND HISTORY OF OFFSHORE BENTHIC INVERTEBRATE RESEARCH IN SOUTH AFRICA

1.1. Introduction

Continental South Africa has a coastline of 3 650 km with an Exclusive Economic Zone (EEZ) of just over 1 million km^2 and is colonised by a rich and diverse marine biota, currently numbering 12 914 described species (Griffiths *et al.*, 2010). However, the quality of the data that have been used to make this biodiversity estimate differ considerably, both among taxa and with respect to habitat, particularly depth. Griffiths *et al.* (2010) estimate that 7 500 additional marine species from the region would need to be described simply to bring the state of knowledge up to the current European level, which is itself far from complete.

1.1.1. Oceanography

The South African coastline is dominated by two major current systems: the coldBenguela Current along the Atlantic coast to the west and the warm Agulhas Current along the Indian Ocean to the east. The Benguela Current comprises firstly an offshore oceanic flow forming the eastern limb of the South Atlantic Subtropical Gyre which has a slow, broad flow towards the equator of only 0.1 – 0.3 m.s^{-1} (Shannon, 1985), with mean sea surface temperatures between 15.4℃ to 20.1℃ (Taunton-Clark and Shannon, 1988). Secondly an inshore dynamic wind-driven upwelling, tempered by local weather systems, results in upwelling cycles lasting 5 – 10 days and occurs mainly in the austral spring and summer (Shannon and Nelson, 1996). The temperatures of this nearshore upwelling region range between 10℃ to 18℃ (Shannon et al., 1992). This intense upwelling along the west coast results in high primary productivity, which in turn supports large fish stocks, including pilchard, anchovy, hake, and rock lobster, each forming the basis for commercial fisheries (Griffiths et al., 2010). The majority of the organic matter related to this high productivity sinks onto the wide continental shelf, where the resultant decay causes a marked drop in the dissolved oxygen content of the bottom waters (Bailey, 1990). At times, mass mortalities of fish, rock lobster and other invertebrates result due to the afore mentioned low-oxygen conditions extending inshore, reaching the shoreline itself (Cockcroft, 2001).

The warm Agulhas Current along the East Coast is made up of nutrient poor, tropical waters southward from the equatorial Indian Ocean. At the shelf break the current flows at its strongest, up to 2 m.s^{-1} and temperatures are high, ranging between 20℃ to 28℃ , depending on season (Lutjeharms, 1998). The current flow close to the shore off northern KwaZulu-Natal and moves further offshore as the shelf becomes wider off Durban (Schumann, 1987). South of East London the current shifts offshore, following the edge of the Agulhas Bank (Grundlingh, 1983) and finally retroflects south of the country. Occasionally, the current reverses and forms pockets of cooler water inshore which flows northward along the coast

(Lutjeharms, 1998). These cool water pockets are unpredictable farther eastward, however on the South Coast between Cape Agulhas and Port Elizabeth they are frequent and predictable. Near the shore, warm surface layers extend over cool bottom waters during summer (Schumann and Beekman, 1984), however winter storms mix the water well, braking down the stratification. At times local, wind-driven upwelling of cool bottom water occurs along regions of the South Coast and where the shelf widens to form the Auglhas Bank the current's fast flow drives upwelling of deep waters (Lutjeharms et al., 1988). There are few commercial fisheries on the South Coast due to the low biological productivity. However, the high human population density, results in intense pressure on coastal marine resources.

The Cape Agulhas and Cape Point regions are seen as an area where the South and West Coast oceanographic regimes overlap. Agulhas Rings (large, anticyclonic eddies) nip off into the South Atlantic Ocean where the Agulhas Current retroflects (Lutjeharms and Van Ballegooyen, 1988), this occurs approximately six times per year (De Ruijter et al., 1999). These Rings transport transport Indian Ocean water in a north-westerly direction into the Benguela system at 0.05–0.08 $m.s^{-1}$ (Shannon, 1985)

1.1.2. Biogeography

In terms of habitat, the intertidal and shallow subtidal benthic biota surrounding South Africa is relatively well studied and the majority of macrofaunal organisms in these ecosystems have probably been identified (Gibbons *et al.*, 1999) and the distribution ranges of many species have been mapped (e.g. Branch *et al.*, 1994). These ranges have since been used to demarcate the large biogeographical provinces along the coastline (Emanuel *et al.*, 1992; Bolton *et al.*, 2004, Lombard *et al.*, 2004), and to plot patterns of coastal biodiversity and endemicity (Turpie *et al.*, 2000, Awad *et al.*, 2002).

According to Gibbons (2005), a good understanding now exists of the factors responsible for structuring coastal biological communities on the local scale (e.g. McQuaid and Branch, 1984, 1985; Bustamante *et al.*, 1997, 1999), allowing these habitats to be mapped at high resolution (Jackson and Lipschitz, 1984). However, distinct biotopes (e.g. Connor *et al.*, 1997a, b) have not yet been established for most of South Africa, with the exception of the near shore East Coast region (Sink *et al.,* 2005).

Biogeographic classification has been an important component used in defining MPAs for spatial management (Norse *et al*., 2003; Hughes *et al*., 2007). Coral reefs (Roberts *et al*., 2002) and inshore habitats (Turpie *et al*., 2000; Awad *et al*., 2002) have been selected as priority conservation areas in coastal ecosystems. However, there has been less progress in developing conservation strategies for the offshore continental shelf and shelf-edge regions (Trebilco *et al*., 2011). As a result MPAs have been set up in intertidal and subtidal regions. However, as there is limited information regarding offshore benthic communities, almost no offshore habitat globally, or in South Africa, is currently protected (Lombard *et al.*, 2004).

In comparison to coastal and inshore habitats, the majority of the offshore continental shelf around South Africa has been relatively poorly sampled and as a result comparatively little is known about the biota of this region (Leslie *et al*., 2000). Lombard *et al*., (2004) described this region as the sub-photic zone and divided it into biozones on the basis of light attenuation, surface wave-induced water motion and major depth divisions. The South Africa offshore region supports major industrial demersal fisheries and is also important for oil, gas and diamond (and potentially phosphate) mining (Griffiths *et al.*, 2004). It is an environment dominated by unconsolidated sediments, with scattered rocky outcrops. The marine benthic organisms found in this region are of direct benefit to society as both food sources and as potential pharmacopoeia (Beckley and Van der Elst, 1993; Cochrane *et al.*, 1997; Hunt and Vincent, 2006; Palmer *et al.*, 2008). Benthic organisms also provide indirect benefits to society as ecological stabilizers (Menge *et al*., 1999), as well as contributing to sustained ecosystem services through benthic-pelagic coupling (Ponder *et al*., 2002). In addition, marine benthic systems have recreational, aesthetic and intrinsic value (McArthur *et al*., 2010).

1.1.3. Current state of knowledge

The current state of knowledge of benthic invertebrate biodiversity over the EEZ, which extends for 1 068 660 km² around South Africa, is extremely poor (Griffiths *et al.*, 2010). Existing data comprise about 1 460 dredge, 602 grab and 442 trawl samples, spread over 3 650 km of coastline and predominantly collected from water shallower than 100 m. Unfortunately, marine biodiversity studies have been neglected for a number of reasons. For example, the majority of the marine realm is inaccessible without costly equipment and ship time. Even shallow marginal seas are inaccessible to anyone but qualified divers, while in deep subtidal regions one is usually sampling blind, as the extent of a habitat or assemblage often cannot be determined and boundaries are less distinct than in shallow coastal areas. Marine systems are also open, with many species dispersing over large areas by means of pelagic larvae (Gray, 2000). As a result of the sea's vastness, there is little common experience about natural events that occur in the ocean and most experiments are limited on a spatial and temporal scale (Ray and Grassle, 1991). According to Schalk (1998) the marine realm is not as well studied as the terrestrial realm primarily due the difficulty of obtaining access to the sea (especially at extreme depths), the vagueness of three-dimensional biogeographic borders, and the fact that the area of marine ecosystems is more than twice that of terrestrial environments. Furthermore, the open sea's lack of distinct ownership makes it complicated for governing bodies to grant rights to research (Attwood *et al.*, 1997).

The threats to intertidal and shallow-water biodiversity are also relatively well understood, and as a result it is possible to project the effects of climate change on its integrity (Stefani, 2000; Mead *et al.,* 2011). Severe stress due to human impact has been on the increase in various marine ecosystems (Griffiths and Branch, 1997; Myers and Worm, 2003; Roberts, 2003; Griffiths *et al.*, 2004; Sala and Knowlton, 2006; Worm *et al*., 2006; Halpern *et al*., 2008; Nellman *et al*., 2008; Costello *et al.*, 2010); however, the development of conservation and restoration strategies to mitigate human impacts has only evolved in the

last decade (Trebilco *et al*., 2011). In light of the above, it is possible to identify priority sites for both inter-tidal and shallow subtidal Marine Protected Areas (MPAs) using actual biological data (Turpie *et al.*, 2000; Awad *et al.*, 2002), although these data were not in fact used in the designation of most sites in the present MPA network along the coast of South Africa (Attwood *et al.*, 1997). This MPA network largely pre-dates these analyses and currently covers approximately 23% of the South African coastline (Gibbons, 2005).

The South African coast has been divided by various studies into between two and five broad biogeographic provinces, with disparities concerning the areas, levels of dissimilarity between regions, region boundaries, and the recognition of overlap zones (Stephenson, 1939; Stephenson, 1944; Stephenson, 1948; Stephenson and Stephenson, 1972; Brown and Jarman, 1978; Emanuel et al., 1992; Stegenga and Bolton, 1992; Burtamante and Branch, 1996; Bolton and Anderson, 1997; Turpie et al., 2000; Sink, 2001; Bolton et al., 2004). Lombard et al. (2004) has amalgamated all existing information and by using expert input, they have described nine marine bioregions (including the previously recognized coastal zones and newly defined offshore zones. The offshore bioregion boundaries are based on minimal biological sampling and therefore may be revised as more quantitative biological field data become available (Griffiths et al., 2010).

Various studies (Emanuel et al., 1992; Turpie et al., 2000; Bolton et al., 2004; Awad et al., 2002) have described the spatial patterns of species richness and endemism of coastal fishes, macroalgae and a variety of benthic invertebrate groups found along the South African coast line. These studies determined that certain taxa such as fishes, bivalves, gastropods, brachyurans and echinoderms become increasingly species rich as one moves further east to a warmer environment. Other groups including amphipods, isopods and polychaetes were found to reach their maximum species richness in the temperate southwest region. If all the groups are amalgamated a pattern of low specie richness occurs along the entire West Coast, while the remaining coast line displays a relatively even species richness. The decrease in species evident to the extreme east is almost certainly due to reduced sampling intensity in that region (Griffiths et al., 2010). According to Griffiths et al., (2010) the South Coast's high overall endemicity is probably due to the way endemism is defined i.e. confined to political borders of a single country, as the proportion of endemics increase linearly from the closest political border.

The faunal composition of the benthic environment is strongly related to the nature of the substratum, and as a result the pattern of distribution of the fauna on rocks differs from that on soft sediments, with areas of high species richness often being associated with high habitat heterogeneity (Gladstone, 2007). This means that there is a greater variety of habitat types available along inshore coastal regions, which promotes high species richness. Deep water benthic richness occurs regardless of low biomass (Snelgrove, 2001), due to the fine scale shifts in sediment or water composition in benthic habitats, which otherwise appear homogenous (McArthur *et al*., 2010). The lack of data for the South African offshore region severely constrains the ability of scientists to evaluate patterns of benthic biodiversity of the region.

As a further complication, it is estimated that, in South Africa, 7 590 of the macrofaunal species of the benthos still need to be formally described, making it difficult for scientists to assess patterns of benthic biodiversity (Griffiths *et al.*, 2010). This, in turn, compromises their ability to fulfil the demands of international biodiversity agreements.

1.1.4. Marine protected areas

The need for a comprehensive, detailed and globally consistent marine biogeography has been recognized for many years (Spalding *et al.*, 2007). In South Africa, the requirements for representative approaches to MPA designation in various national, regional and global planning commitments and legal frameworks have provided added urgency to this need (Spalding *et al.*, 2007). Existing global classification systems in the marine environment are restricted in their spatial resolution. According to Spalding *et al.* (2007), some are inconsistent in their spatial coverage or methodological approach, while the few publications that have attempted to use biogeographic regionalization in global marine conservation planning (e.g. Kelleher *et al.*, 1995; Olson and Dinerstein, 2002) have been qualitative and have expressed concern about the lack of an adequate global classification. The faunistic (biogeographical) zones that have been identified around South Africa (Lombard *et al.*, 2004) are not based on biological analysis, but are defined by expert opinion based on physical criteria (Griffiths *et al.*, 2010). Therefore, data are required to support offshore spatial planning (e.g. to enable informed decisions as to the environmental impacts of granting mining or fishing concessions in these benthic habitats) and to identify potential offshore MPAs based on biodiversity patterns and features. If there is little biological information available for an area, or where logistical constraints preclude biological sampling, diversity may be assessed using an abiotic surrogacy (Lombard *et al*., 2004; McArthur *et al*., 2010), i.e. using data of temperature, oxygen concentration, salinity and sediment composition, which all directly influence benthic organisms (Snelgrove, 2001), to estimate possible diversity of the benthos. The Convention on Biological Diversity's Program of Work on Protected Areas and the Ramsar Convention on Wetlands are international agreements that require biogeographical classification for developing ecological representative systems of protected areas. According to Chape *et al.,* (2005), only 0.5% of the ocean's surface is protected at present, which is an extreme underrepresentation.

The core idea underpinning the term "representative marine reserve" is the protection of a full range of biodiversity globally i.e. genes, species and higher taxa along with the communities, evolutionary patterns and ecological processes that sustain this diversity. Biogeographic classification provides an essential foundation for the assessment of representativeness (Olson and Dinerstein, 2002; Lourie and Vincent, 2004). Biodiversity encompasses a series of different levels of organization, from the genetic variation between individuals and populations to species diversity, assemblages, habitats, landscapes and biogeographical provinces (Gray, 2000). According to Spalding *et al.* (2007), biogeographic regions form natural frameworks for marine zoning, which is a tool increasingly used by regional management organizations.

The aim of this chapter and the motivation behind this thesis, is to demonstrate the lack of data that exists for the offshore regions of South Africa and the need to collect adequate biological data sets.

1.2. Historical overview of benthic marine invertebrate research in South Africa

The knowledge of the diversity of benthic invertebrates in the sub-photic zone is almost totally qualitative, and is based on scattered samples that were collected during the Great Expeditions (late 1800's and early 1900's) of the *Challenger*, *Gazelle*, *Valdivia* and *Gauss*, or by Gilchrist, Barnard and others from the *Pickle* and *Pieter Faure* (early 1900's), and more recently (1950's - 1970's) from the University of Cape Town (UCT) Ecological Survey and the *Meiring Naude* cruises (Louw, 1977, 1980). Today, the only benthic invertebrates (targeted crustaceans excepted) that are routinely collected in the sub-photic zone are those caught incidentally during demersal trawls (until the inception of the present study) and, with a few exceptions, these were simply discarded without comment (R. Leslie, personal communication).

Table 1.1. Historical cruises that collected a broad selection of invertebrates offshore in South African waters.

			Number of Samples		
Date	Location/Ship	Depth (m)	Dredge	Grab	Trawl
1873 – 1876	H.M.S. Challenger	179 - 4 252	5	0	0
1874	Gazelle	90	2	0	0
1898	Deutchen Tiefsee Expedition	70 – 2 750	13	0	0
1898 – 1906	Pieter Faure	11 - 475	44	0	91
1925 – 1927	Discovery Expedition	47 - 550	1	0	3
1934	DANA Expedition	1 000 - 3 000	0	0	3
1946	Langebaan, UCT	2.5 - 9	118	0	0
1946 – 1948, 1950 – 1951	False Bay, UCT	9 - 175	238	0	0
1946, 1953, 1959, 1969, 1962 – 1964	Saldanha Bay, UCT	4 – 56	109	110	0
1946 – 1954, 1956 – 1958, 1963	South African coast, non-commercial trawler material	5 - 768	20	0	106
1947 – 1949	Africana II Deep-sea	9 - 547	71	0	30

1950 – 1952	Galathea	425 - 5 220	5	25	6
1954	Algoa Bay, UCT	8 – 39	12	0	0
1956	Mossel Bay, UCT	8 – 31	44	0	0
1956, 1958 – 1962	South Coast, UCT	7 - 325	239	115	5
1957	Lamberts Bay, UCT	8 – 29	27	0	0
1958 – 1959, 1963 - 1964, 1967 – 1968	Natal, UCT	18 - 200	11	16	10
1959 – 1964	West Coast, UCT	11 – 1 240	54	39	0
1959 – 1962, 1964, 1965, 1967	False Bay, UCT	4 - 100	321	217	0
1967	False Bay, UCT	4 - 102	0	35	0
1970	Langebaan Transect, UCT	13 - 600	17	17	0
1972 – 1973	Still Bay Shelf Transect, UCT	10 - 550	62	47	1
1976 – 1979	Meiring Naude	40 – 1 950	47	0	43
1980	Table Bay, UCT	8 – 97	0	0	125

Cruises reviewed in this chapter date back as far as 1873, with the most recent one being conducted in 1980 (Table 1.1). During this period 2 504 benthic samples were collected, comprising 1 460 dredge, 602 grab and 442 trawl samples (Figure 1.1). The depth distribution of the South African EEZ is depicted in Figure 1.2. It should be noted that the majority of samples were collected from <100 m depth, with sample intensity declining rapidly with increasing depth (Figure 1.3). In the 0 - 100 m depth interval, a total of 2 049 samples were taken (equivalent to 39 samples per 1 000 km²; Figure 1.4), the greatest number of samples taken in any depth interval (Figure 1.3), but still a very small number on which to base community-level analyses. The 100 - 200 m depth interval has a considerably lower total number of samples (184), while all other depth intervals (between 200 and 5700 m) have less than five samples per 1 000 km² (Figure 1.4).

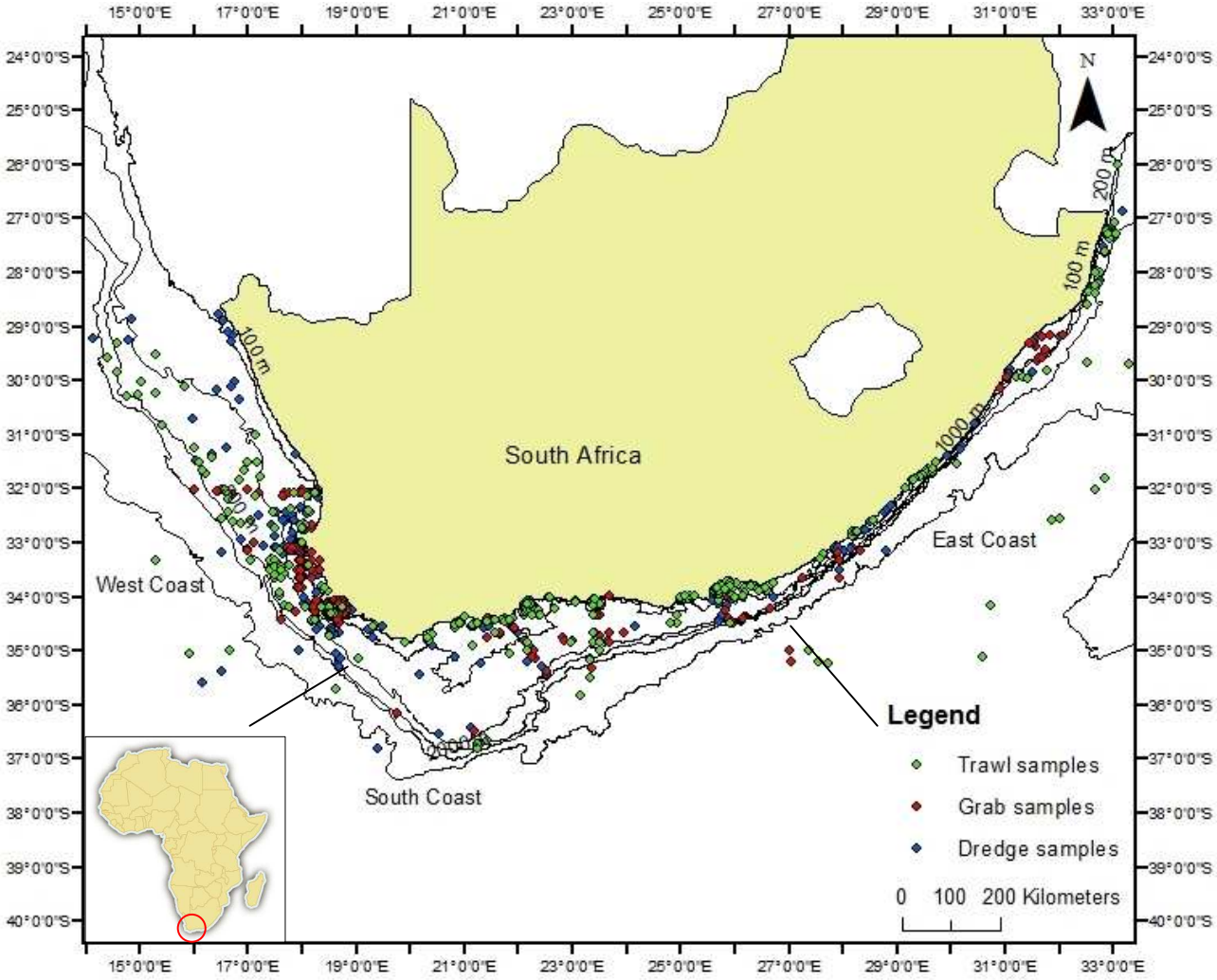


Figure 1.1. Map depicting the locations of the benthic community samples collected around South Africa from 1873 to 1980. The insert in the left hand corner depicts the continent of Africa with the sampling region circled in red.

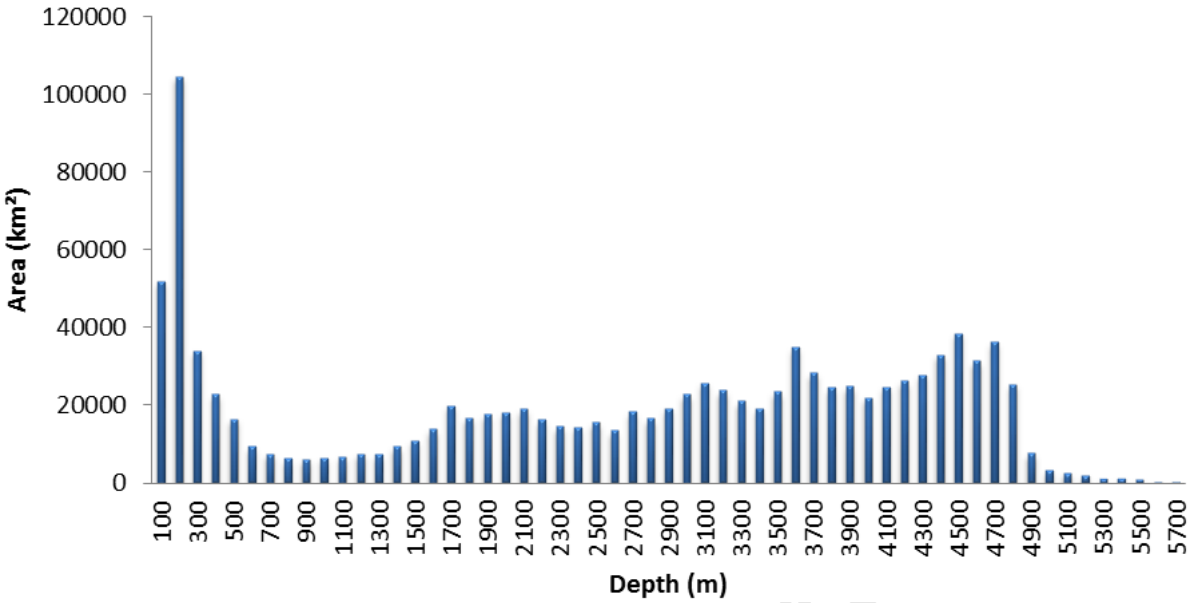


Figure 1.2. The total area (km^2) of each 100 m depth interval in the Exclusive Economic Zone surrounding South Africa.

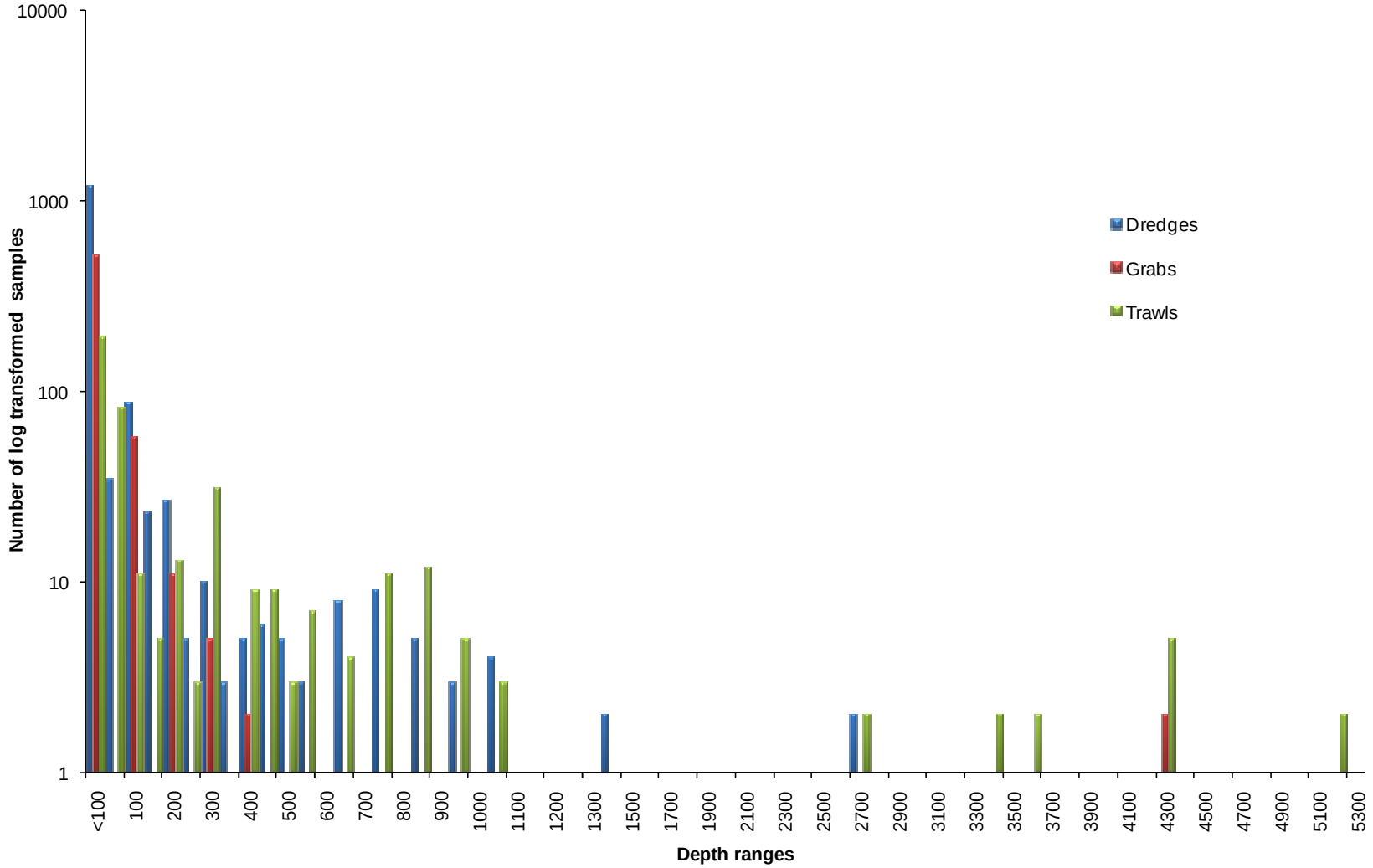


Figure 1.3. The number (log transformed) of historical samples (1873 to 1980) collected in South African waters at each depth interval using the three different types of gears.

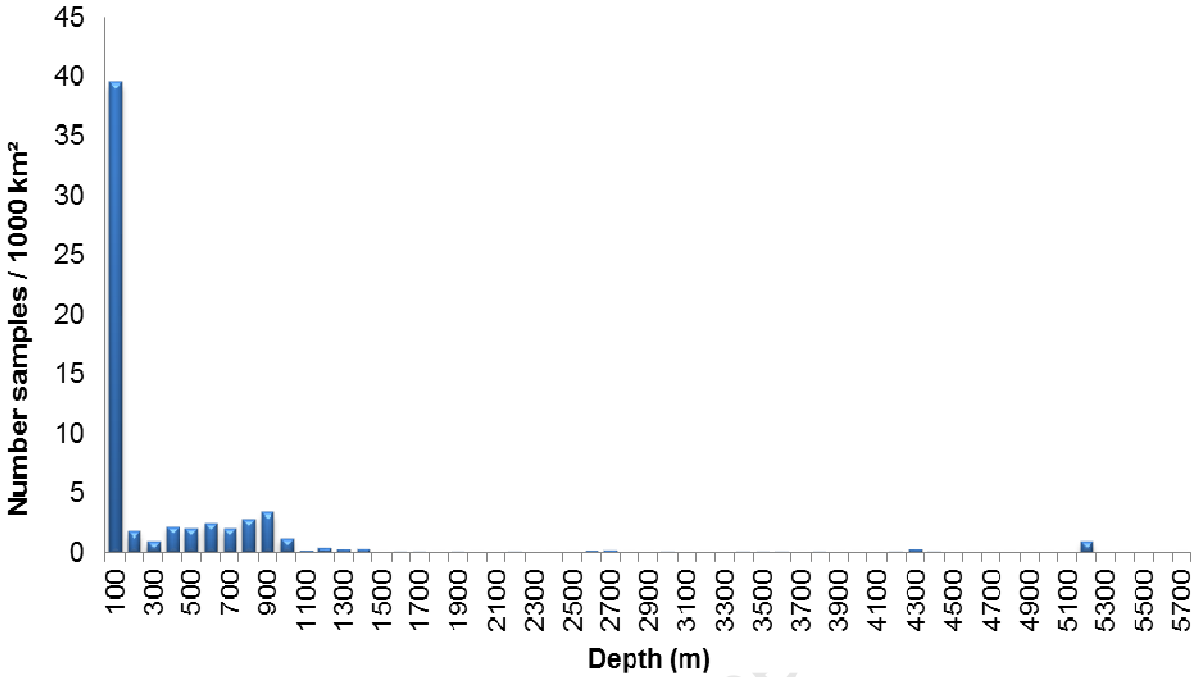


Figure 1.4. Number of samples per 1 000 km² collected in each depth interval along the South African coast during the research cruises conducted from 1873 to 1980.

The first benthic samples collected in South African waters were the five dredges conducted during the British *Challenger* Expedition in December 1873, at depths ranging from 179 - 4 252 m (Table 1.1). Following this, the *Gazelle* collected two dredge samples at a depth of 90 m in 1874 (Table 1.1). The first South African ship to collect benthic samples was the *Pieter Faure* over the period 1898 - 1906. During this period, 44 dredges and 91 trawls were collected in depths of 11 - 475 m (Table 1.1). The *Deutchen Tiefsee Expedition* occurred in 1898 in South African waters and collected 13 dredges at depths of 70 - 2 750 m (Table 1.1).

The subsequent benthic samples were only collected 27 years later during the *Discovery Expedition* in 1925 – 1927, in which one dredge sample (at 47 m) and three trawl samples (between 250 - 550 m) were collected (Table 1.1). Shortly after this the Danish *Dana Expedition* collected three trawl samples at depths of 1 000 - 3 000 m in 1934 (Table 1.1). During 1950 - 1952 the Danish deep-sea expedition, this time aboard the *Galathea*, collected 36 samples in South African waters. These consisted of five dredge, 25 trawl and six grab samples at depths between 425 - 5 220 m (Table 1.1). Finally, from 1976 - 1979 the South African *Meiring Naude* collected 47 dredge and 43 trawl samples at depths between 40 - 1 950 m (Table 1.1).

The end of the 1940's saw a marked increase in benthic sampling in South African waters as a result of the initiation of the benthic sampling programme known as the 'University of Cape Town's (UCT)

Ecological Survey', which took place in a number of regions (Table 1.1). Dredge samples were collected at Langebaan in 1946 in shallow waters (2.5 - 9 m). Then in 1958 the UCT bought an old wooden trawler (*John D. Gilchrist*), which enabled the collection of deeper sub-photic benthic samples in subsequent years. A wide range of dredge, grab and trawl samples were collected with the trawler, including samples taken in False Bay between 1950 and 1964; in Lamberts Bay in 1957; in Saldanha Bay in 1953 - 1964; along the South Coast from 1956 - 1962; off the West Coast in 1959 - 1964; off the Natal coast from 1958 to 1964; off Mossel Bay in 1956; and in Algoa Bay in 1954 (Table 1.1). Between 1947 and 1949 the then Marine and Coastal Management used their research vessel the *Africana II* to collect 30 trawl and 71 dredge samples at depths of up to 547 m (Table 1.1). In 1965 UCT replaced the wooden trawler with a well-equipped, custom-built research vessel, the *Thomas B. Davie* (Day, 1977). With this ship, the University collected dredge, grab and trawl samples in False Bay in 1967; offshore of Natal between 1967 and 1968; offshore of Langebaan in 1970; and finally in Table Bay in 1980.

The temporal sequence of samples collected from all these sources combined is shown in Figure 1.5 and indicates one main period of activity during the 1960's. The majority of UCT Ecological Survey samples were collected in the 1960's (Table 1.1 and Figure 1.5), during which time almost 600 dredge, and just under 500 grab samples, were collected. During this same period only 11 trawl samples were collected (Figure 1.5) The collection of grab samples was only initiated in the 1940's, compared to dredge surveys which were already being conducted in 1870.

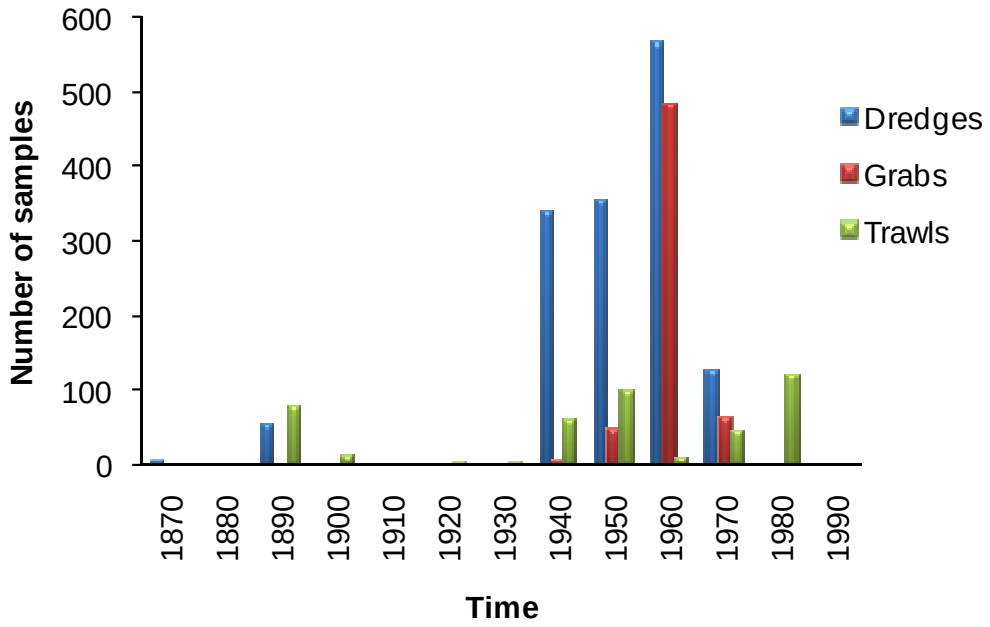


Figure 1.5. Numbers of invertebrate samples collected in South African waters for each decade from 1870 to 1990 using the three types of sampling gear used for historical offshore surveys.

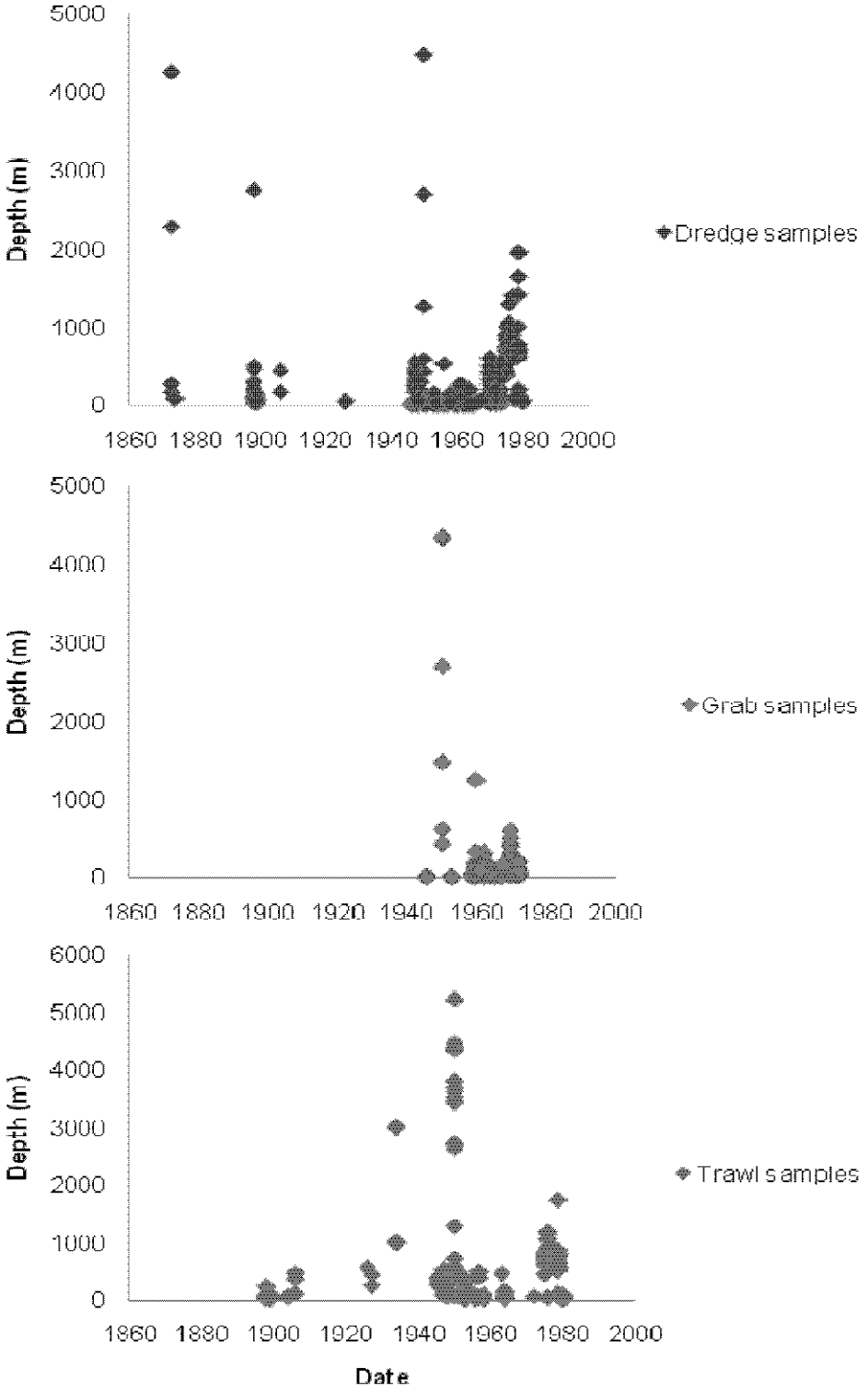


Figure 1.6. The relationships between date and sampling depth for samples collected using each of the three main gear types, from 1870 until 2000.

Figure 1.6 shows the depth ranges of samples collected by the various sampling methods for each decade. The historical collections taken before 1940 were exclusively trawl and dredge samples. It is interesting to note that very deep samples (>4 000 m) were collected as early as 1879 and only again in 1950. The grab samples were all collected in the 1960's and 1970's, after which the surveys ended, while most of the trawl samples were taken before the 1960's and in water deeper than 100 m (Figure 1.6). The dredge samples were more widely spread over the years, and were all collected in less than 1 000 m of water (Figure 1.6). By the late 1980's benthic sampling had come to a complete halt as UCT sold its research vessel and did not acquire a new one to replace it. However, when looking at guide books for benthic invertebrates, specifically hydroids (Millard, 1975), inshore and offshore gastropods (Gosliner, 1987; Richards, 1989; Steyn and Lussi, 2005), crustaceans (Barnard, 1950), amphipods (Griffiths, 1976) and isopods (Kensley, 1978), the rate at which species were described continued to increase over time, as these old collections were 'mined' by taxonomists.

Examining the samples collected along the South African coast by region, it was noted that they were primarily sampled by dredges; 966 samples on the West Coast, 388 on the South Coast and 47 on the East Coast (Figure 1.7). Grabs were overall the second most used manner of collection with 421 grabs on the West Coast, 148 on the South Coast and 33 on the East Coast. Trawls were the main sampling method only along the East Coast, with 97 trawls, while there were 116 on the West Coast and 226 on the South Coast. Overall the West Coast had the most and the East Coast had the least number of samples of all three regions, while the South Coast was the most evenly sampled in terms of the three sampling methods.

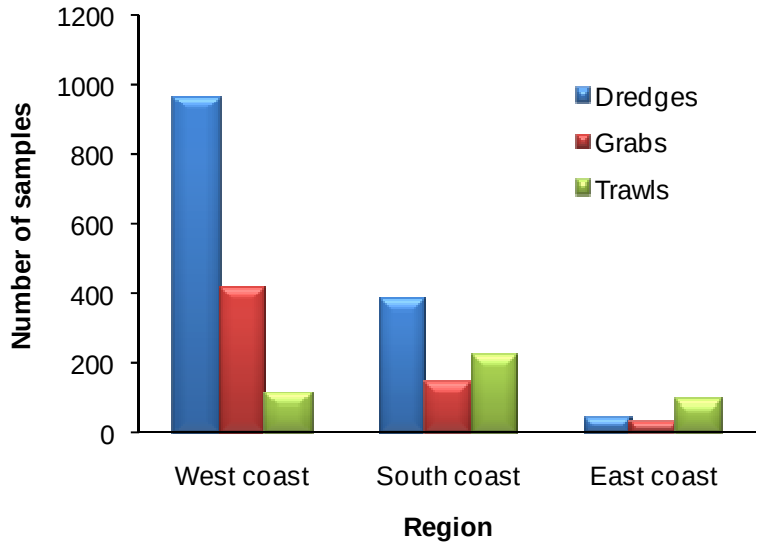


Figure 1.7. Number of benthic samples collected from the West Coast, South Coast and East Coast regions of South Africa using the three different gear types.

The above-mentioned surveys were all catalogued and the vast majority of the samples were stored at the Iziko South African Museum in Cape Town, South Africa. These surveys have contributed to numerous subsequent research theses and peer-reviewed journal publications, including analyses of transects off Lambert's Bay (Christie, 1974), False Bay (Field, 1971) and Saldanha Bay (Kruger *et al.*, 2005). A large number of taxonomic publications (Barnard, 1950; Millard, 1966, 1975; Christie, 1976; Millard, 1977) and books (Day, 1967, polychaetes; Clark and Courtman-Stock, 1976, echinoderms; Griffiths, 1976, amphipods; Day, 1978, cumaceans; Kensley, 1978, isopods; Gosliner, 1987, nudibranchs; Richards, 1989, gastropods; Steyn and Lussi, 2005, gastropods) were also based largely on these surveys. However, these previous works were either taxonomic in nature or analysed data from one transect running from inshore to offshore, while no large-scale regional analysis exists and thus the community patterns for the whole region have not yet been assessed.

Historically, most samples have been taken in waters shallower than 100 m (Figures 1.2, 1.3, 1.5 and 1.6), and either looked at a specific taxonomic group, or all taxa for a specific site/transect. This has left a large gap in the knowledge of offshore benthic biodiversity. This thesis aims to examine community structure on a broader geographic scale and across taxa. In addition, the quantitative invertebrate samples that have been collected in the offshore region have largely not been analysed for community structure (Day, 1978); or have been published only in the grey-literature (Field *et al*., 1995, 1996; Gibbons and Sulaiman, 1998; Gibbons and Goosen, 2002). While these data may provide a base that can be consolidated with data that may be generated from future surveys, their spatial extent is currently too limited to be useful from a conservation point of view.

Whilst distributions of the majority of species found in the offshore benthic environment have not been mapped, the general distribution of habitats in the sub-photic zone has been mapped (at low resolution) based on their general sedimentary environment (Dingle *et al*., 1987) and surficial sediment texture (e.g. Birch *et al*., 1986). The habitat of a species is, however, more complex than just sediment type and distribution. Oceanographic features, water mass properties and nutrients also contribute to habitat. For conservation planning purposes, it is assumed that the different habitats support different biota and that the habitats act as surrogates for biodiversity. Units for conservation are then identified on the basis of their representation in different assumed biogeographic provinces (Lombard *et al.*, 2004). The biogeographic provinces are 'assumed' due to the fact that there is no empirical study that delimits the number, extent or affinity of regional sub-photic biogeographic zones around South Africa. Whilst the use of sediment type as a surrogate for the fauna is based on an acknowledged relationship between the characteristics of sediment and its associated fauna (e.g. Lu, 2005), this has not been tested locally and there is a need to check the accuracy of biotic surrogacy for the different habitats in the different biogeographic regions.

Over the last decade, a large proportion of marine ecosystems have come under severe stress from increasing human impacts, such as commercial fishing, marine transportation and land-based activities (Myers and Worm, 2003; Roberts, 2003; Sala and Knowlton, 2006; Worm *et al*., 2006; Halpern *et al*., 2008; Nellman *et al*., 2008; Ban *et al*., 2010). In order to protect biodiversity, it has been recommended that nations set aside between 20 - 23% of each different habitat as protected areas (World Parks Congress, 2003). The South African National Spatial Biodiversity Assessment shows that, with the exception of the sub-photic zone along the extreme north-east coast, the balance of the deep sea benthic system across the region is either not legally protected or is "hardly protected" (Lombard *et al.*, 2004). This lack of protection is a cause for concern that will only become more exaggerated in the future, as the prime threats to the integrity of this system, i.e. extractive marine living resource use (EMLRU) and mining, are anticipated to increase (Lombard *et al.*, 2004). The author suggests that the sub-photic zones along the West and South Coasts of South Africa should be prioritised as urgent areas for protection (where 1 refers to highest priority and 6 refers to the lowest priority). In general, Lombard *et al.* (2004) recognized a systematic study of the deep benthic biodiversity to be one of the top ten priorities for future research, and soft-bottom trawling ground and mining areas to be two of the three most threatened habitats in need of conservation. A study of the United Kingdom marine ecosystems showed a decline in biodiversity leading to a proposed change in the provision of goods and services, reduced resilience and resistance of species and ecosystems to change, loss of marine environmental health, decline in fisheries potential, and recreational opportunities (Beaumont *et al*., 2008). It is thus vital that the offshore regions of South Africa need to be rapidly researched and protected, possibly with the help of abiotic surrogacy.

A significant proportion of the EEZ is almost completely un-sampled, making any biogeographic analysis virtually impossible. Although the 259 301 km² area of the EEZ that is shallower than 1 000 m has been sampled 2 434 times, 92% of these samples were collected at depths <200 m, thus leaving the remaining area (between 200 – 1 000 m) with just 201 samples. The area deeper that 1 000 m, covering a vast 815 970 km² of the EEZ, only has 46 samples. Hence, the South African EEZ is in dire need of being adequately surveyed so that the resources in this area can be effectively managed and representative protected areas can be designated.

1.3. Aims

Although a historical data set for the areas covered in this thesis is available, the lack of a digitised version thereof makes collation of these data a time consuming process. The current project aims to take advantage of a new set of samples that are current and not historical, using a proper stratified grid survey and similar trawling equipment to allow for the data to be compared across surveys. The macrofaunal data collected will be used to determine patterns in the offshore benthos around South Africa, excluding the East Coast. No surveys were conducted along the East Coast during the period of the study, as this region has no large fishing grounds, although crustacean fisheries do occur (Atkinson and Sink, 2008). Furthermore the area does not consist of a large continental shelf, like the West Coast and South Coast,

but rather a narrow continental slope (Lombard *et al.*, 2004). The samples collected for the current study were derived as bycatch from demersal sampling, as this is the only type of sampling currently being conducted, due to the lack of funding for dedicated invertebrate sampling cruises. Given the sampling method available i.e. trawling, only data on the macrofaunal communities of unconsolidated sediments could be collected, as the trawling net would be torn if pulled over hard substratum. The data collected were interpreted in a format that can be used by the authorities and managers, i.e. biogeographic classification, to assist them in the allocation of mining and other permits, as well as to provide baseline information valuable to the selection and management of marine reserves. The project builds upon the expertise in marine invertebrate taxonomy as well as on the existing maps of habitat distribution and the benthic surveys planned by the Department of Environmental Affairs (DEA). Data collected have also been lodged in the Ocean Biogeographic Information System (OBIS) African node (South African Data Centre for Oceanography, Stellenbosch), where it can be accessed and analysed to help determine global biodiversity patterns.

The project further addresses certain priorities of the National Spatial Biodiversity Assessment (Lombard *et al.*, 2004). These include the classification and mapping of marine communities in two of the three marine habitats deemed most in need of conservation, i.e. the sub-photic and continental shelf areas offshore of the West Coast region of South Africa (Lombard *et al.*, 2004). It should be noted that in keeping with Rice *et al*. (2011), marine biogeographic classifications contain boundaries that are generalized and not precise and should not be interpreted as 'hard' management lines.

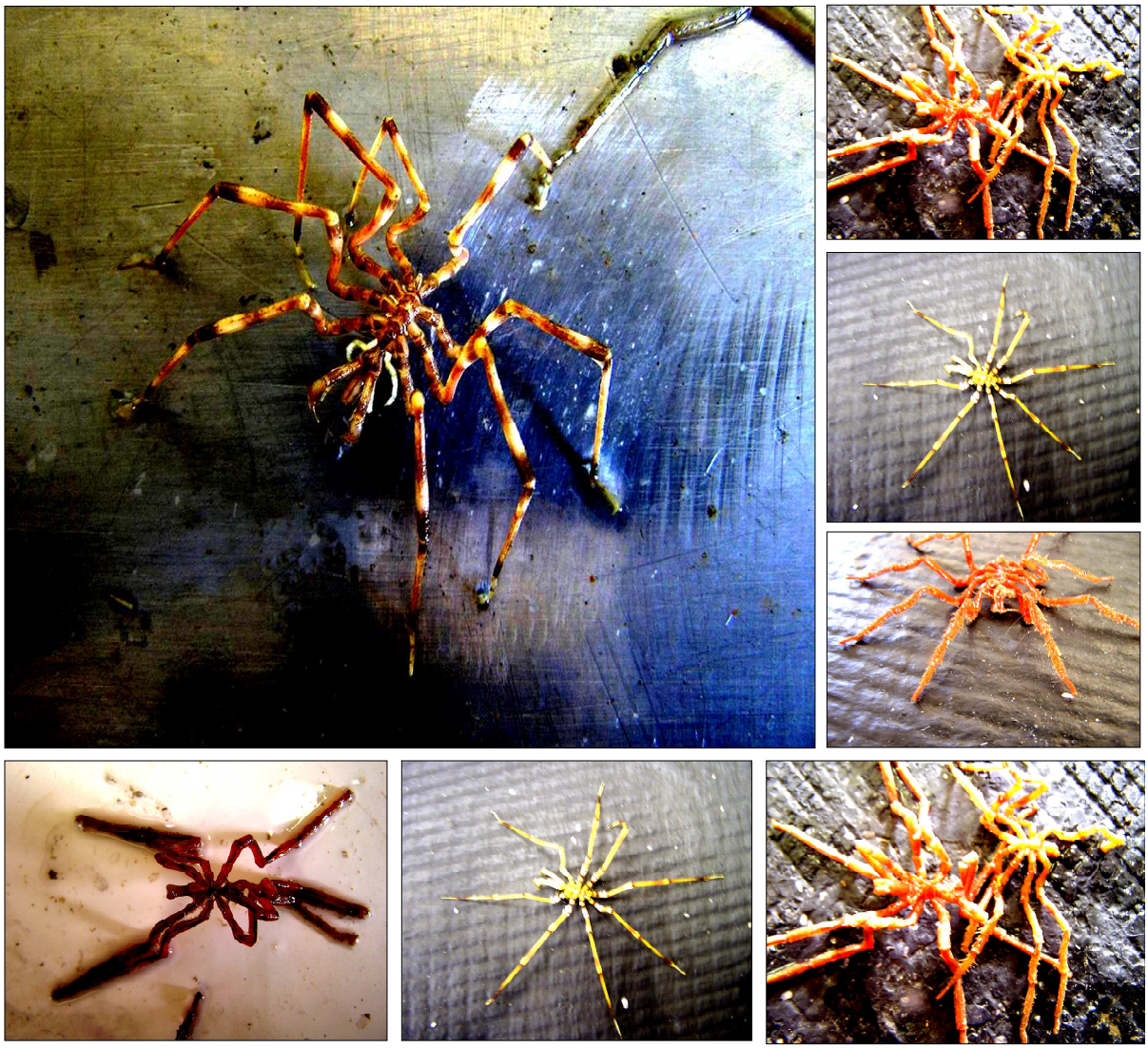
This thesis comprises of two studies that will be used to identify the number and location of identifiable communities/groups that may warrant conservation. This will be discussed in Chapter 4. Biogeographic classification has been used to support the analyses of biodiversity patterns and ecosystem processes, even for areas where knowledge is lacking (Rice *et al*., 2011). Biogeographic classification is currently being used to select conservation regions, such as MPAs, and to manage the marine biodiversity in offshore regions (Rice *et al*., 2011). Chapter 2 presents the findings from the survey that took place along the West Coast of South Africa aboard the R.V. *Dr. Fridjof Nansen*, while Chapter 3 presents the findings from the surveys that took place along the West Coast and South Coast of South Africa aboard the *F.R.S. Africana*.

Rice *et al*. (2011) stated that marine biogeographic classifications have been based on either biological information (e.g. known distribution of certain species) or edaphic environmental variables (such as bathymetry, water masses, currents, substrate, nutrients and oxygen levels) or a combination of both. These approaches delineate groups of flora and fauna, and physical features and processes that are relatively distinct or different from adjacent areas. McArthur *et al*. (2010) noted that the biological information has the greatest power to detect relationships of species distribution with abiotic variables. The author will be using the biological method to partition ecological units or communities to form a baseline that can then be used to determine which environmental variables have the most significant

effect on the benthic macro-fauna distribution pattern. The biogeographic classification determined for the benthic communities in Chapters 2 and 3 can then be built upon and used for further research studies to identify the most valuable areas in terms of species richness where MPAs should be incorporated (Chapter 5).

The final chapter synthesises the results of the previous three chapters and discusses the use of the biogeographic classification method. This chapter also provides recommendations for determining MPAs offshore of South Africa and advises on future research.

Chapter 2



LARGE-SCALE SPATIAL PATTERNS WITHIN BENTHIC INVERTEBRATE ASSEMBLAGES ALONG THE WEST COAST OF SOUTH AFRICA BASED ON THE NANSEN TRAWL SURVEY

2.1. Introduction

This study takes advantage of invertebrate macrofauna caught as bycatch during a demersal fish survey conducted along the West Coast of South Africa and plots their distribution patterns. These patterns are then analysed to determine whether relationships exists with the gradients of environmental variables, including depth, temperature and oxygen. It has been noted that organisms react to their habitat at the species level (Bertrand *et al*., 2006), thus species level datasets will be the most powerful to identify relationships with abiotic variables.

Benthic invertebrate macrofauna play a vital role in structuring entire benthic communities through interactions such as competition, predation and bioturbation of surface sediments (Smith *et al.*, 1986; Ventura *et al.*, 2001). These important benthic invertebrates include suspension feeders and detritivores, which play an active part in recycling and remineralisation. In addition, macrobenthos act as a food source for fishes and other marine organisms (Bandelj *et al.*, 2009). They are also an important resource for the world's fisheries, especially in regions of high pelagic productivity (Postma and Zijlstra, 1988; Caddy, 1989; Pauly *et al.*, 2002) such as the Benguela Upwelling System off the West Coast of South Africa, where this study took place.

Conroy and Noon (1996) noted that the distribution of benthic species, as well as their biodiversity, is poorly known. According to Spalding *et al.* (2007), the goal of a representative reserve system is to protect a wide range of biodiversity worldwide, including genes, species and higher taxa; together with their communities, evolutionary patterns and the ecological processes that maintain this diversity. Identifying and establishing the borders of MPAs is often confounded by competing demands for other resources in those areas (such as fish, minerals or oil) and by geopolitical and institutional problems, including national or state boundaries (Ward *et al.*, 1999).

Biogeographic classifications are fundamental to developing protected area networks that are ecologically representative; as required by international agreements like the Convention on Biological Diversity's Programme of Work on Protected Areas Network (Spalding *et al.*, 2007). Furthermore, biogeographic classification is the foundation for the assessment of representativeness within these areas (Olson and Dinerstein, 2002; Lourie and Vincent, 2004).

In South Africa information on the distribution of deep sea invertebrates is sparse and limited to certain taxa, such as Crustacea (Beyers, 1994) or fish (Turpie *et al.*, 2000), which are relatively easy to identify and/or play an important ecological role in macrofaunal communities. Furthermore, most studies on deep

sea invertebrates are of a taxonomic nature, often restricted to taxon-by-taxon studies (Barnard, 1950; Millard, 1966; Day, 1967; Millard, 1975; Clark and Courtman-Stock, 1976; Griffiths, 1976; Day, 1978; Kensley, 1978; Gosliner, 1987; Melville- Smith, 1988; Beyers, 1994). Benthic invertebrate biogeography studies typically cover isolated transects (Field, 1971; Christie, 1976; Kruger *et al.*, 2005) which identify depth-delineated communities, or are only taxon specific (Hiller, 1994; Turpie *et al*., 2000; Bolton *et al*., 2004), giving no indication of the wider distribution patterns of the deeper benthic invertebrate fauna. Since we have a poor appreciation of the number and distribution patterns of benthic marine communities/groups, we are unable to plan a representative network of offshore marine protected areas (MPAs).

This lack of knowledge results in groups/communities being assumed based on sediments or depth (Lombard *et al.*, 2004). However, according to Snelgrove and Butman (1994), soft-sediment communities are complex and may need more than a single environmental variable to define them. Due to this, it is advantageous to use actual benthic invertebrate megafuana data to determine species distribution patterns, rather than using abiotic surrogates. During the Nansen survey, which was designed to survey demersal fish stocks, an opportunity arose to collect a series of samples of benthic invertebrate megafuana that were collected as bycatch. The analyses of these data allowed a rare insight into the offshore benthic invertebrate megafuana distribution patterns of South Africa.

2.2. Study Area

This study was based on the West Coast biomass survey conducted by the *R/V Dr Fridtjof Nansen* which covered the area from Cape Agulhas (34° 49'S, 20° 0 0'E) to the South African border with Namibia (29° 42'S, 17° 59'E), and from the coastline to the 700 m isobath (Figure 2.1). Spatial distribution of sample sites were plotted using a Geographical-Information System (GIS), ArcGIS 9, with actual trawl positions reported in decimal degrees.

This cold temperate region is dominated by the Benguela Current, which is the eastern boundary current of the South Atlantic subtropical gyre (Peterson and Stramma, 1991; Wedepohl *et al.*, 2000), beginning as a northward flow off the Cape of Good Hope, then skirting the western African coast towards the equator. The sources of the Benguela Current include Indian and South Atlantic subtropical thermocline water; saline, low-oxygen tropical Atlantic water and cooler, less saline sub-Antarctic water (Gyory *et al.*, 2004). This region, also known as the Benguela Ecoregion, has a large continental shelf that widens near the Namibian border. As a result, this area exhibits frequent upwelling of deeper, nutrient-rich, cold water that forms the basis of a rich food chain (Gyory *et al.*, 2004). In contrast to other major upwelling systems, the Benguela comprises large hypoxic and anoxic shelf areas, which have strong influences on the recruitment strategies of certain species such as hake inhabiting these areas (Woodhead *et al*., 1998). The low oxygen variability is mainly determined by local seasonal wind characteristics and minimal forcing (Monteiro and Van der Plas, 2006).

2.2.1. Sampling region

The mean surface area sampled during a tow was 2.363 ha, this was determined using the swept area methodology (ha = 10 000 m^2). The continental shelf runs diagonally across the sampling area on the Nansen West Coast survey.

2.2.2. Habitat classification

During this study the habitat was defined according to Lombard *et al.* (2004), where ecosystems were divided at a relatively broad scale into habitats. The distribution data of benthic macroinvertebrate (epifaunal) species collected during this study were used in the analyses to determine habitat divisions. The number of species in a given space is referred to here as species richness (Magurran, 2004), while species co-existing in a given space are referred to as a community or group (McArthur *et al.*, 2010). Groups/communities represent the fine-scale biodiversity patterns, which are referred to as biotopes by Lombard *et al.* (2004).

2.3. Materials and Methods

2.3.1. Survey

One six-week survey (Jan - Feb, 2007) was carried out on the *R/V Dr Fridtjof Nansen* along the West Coast of South African. A structured, depth-stratified sampling technique was used, in which a grid cell layer was placed over the West Coast region. Using a 5x5 minute grid cell, one sample was taken in a pre-selected grid. Data were mapped onto the 5x5 minute grid cell thus representing their location in space. A total of 99 samples were taken at depths ranging from 85 - 691 m (Figure 2.1). A high-opening demersal shrimp and fish trawl net with Thyborpen trawl doors was employed (31 m headline; 47 m footrope with 0.12 m roller discs; 5 - 6 m headline height; 18 - 22 m mouth opening during towing; 32 mm cod-end mesh with 25 mm cod-end liner).

2.3.2. Swept area

The Nansen survey sampling sites were located between 35° 32'S, 18° 58'E and 29° 36'S, 16° 35'E. The survey was conducted on a North to North-Easterly route, whilse collecting samples from 99 sites. Each trawl sampled a specific surface area, and the equation below was used to calculate the swept area covered by each trawl. This was then converted to hectares (ha) and the abundance and biomass of species based on their density at each station was determined. The following equation was used:

$$\text{Swept area in hectares (ha)} = \frac{[(\text{trawl duration}/60) \times \text{speed of ship}] \times (\text{mouth width of trawl net}/1852)}{342.99}$$

where 1 nautical mile = 1852 m

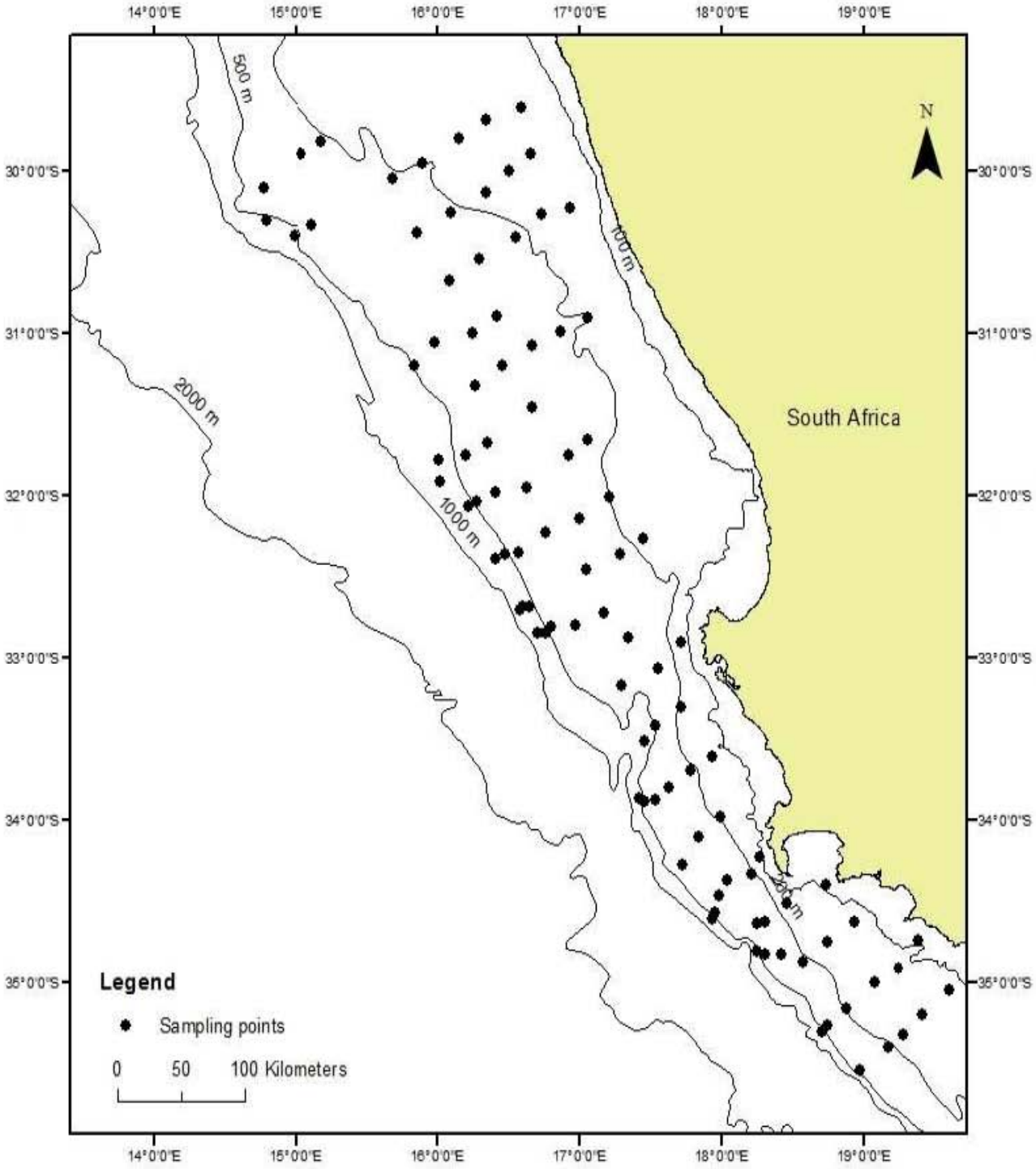


Figure 2.1. The sample points that were surveyed along the West Coast of South Africa during a six week cruise aboard the *R/V Dr Fridtjof Nansen*.

2.3.3. Methodology

The net was dragged along the seafloor for 30 min for each sample and, once on deck, invertebrates were collected from the trawling net. Similarly to Williams *et al.* (2011) macrobenthic invertebrate catches were sorted at sea to the level of operational taxonomic unit (OTU) by a single student. OTU was the best resolution possible with the resources available on the vessel, but effectively differentiated species for many groups. Each OTU was given a unique identifier (name), counted, weighed and a representative sample photographed. In the case of Porifera average individual biomass conversions were used to determine abundance. Certain taxa, such as hydroids and sponges, could not be identified and sorted beyond family or higher level. There were also a number of taxa undifferentiated at lower taxonomic resolution, due to a lack of taxonomic specialists in Africa. Species that could not be identified in the field were preserved in 70% formalin or 95% ethanol for later identification (if possible). I

Depth, together with bottom water temperature (measured in ℃), dissolved oxygen (DO, measured in mg/L) and salinity (measured using the Practical Salinity Scale) were recorded at each trawl station using a conductivity, temperature and depth profiler (CTD). This data was collected generally at 5 m from the bottom during each trawl, weather could have an influence on this exact depth, but not by much (pers. comm. R. Cooper). Surficial sediment texture data were taken from the National Spatial Biodiversity Assessment (Dingle *et al*., 1987 in Lombard *et al.*, 2004), and plotted on a GIS to produce a layer of surficial sediment data that was intersected with the samples plotted in ArcGIS 9. The sediments were divided into eight sediment types according to grain size, from tiny to large (Dingle *et al*., 1987); these types were then classified as gravel, gravelly mud, mud, mud-sand-gravel, muddy sand, sand, sandy gravel and sandy mud.

2.4. Statistical Methods

Total biomass and abundance of each species were recorded for each demersal trawl station. Species that were only recorded once during the entire survey were excluded from statistical analysis, due to the uncertainty concerning their association with the particular environment in which they were recorded. Data were logarithmically transformed, hence they were close to normality.

2.4.1. Hierarchical cluster analysis

Data were analysed to represent communities by graphical description of the relationships between the biota in all the samples, to differentiate sites on the basis of their biotic composition and to relate the biotic patterns to the corresponding environmental variables. This enabled different communities to be distinguished on the seafloor.

Hierarchical cluster analysis was conducted in the statistical analysis programme MINITAB 16.1 to classify the sampling sites into discrete groups based on similarities between their species compositions

abundance. Hierarchical clustering created ranked clusters which were graphically depicted in the form of dendrograms. The closer the proximity of the clusters, the more similar their species compositions, while the farther apart the clusters, the more dissimilar their species compositions. Cluster analysis required the linkage method, distance measure and cut-off points to be selected before the sites could be classified into groups.

The first step of the cluster analysis was to select an appropriate linkage method (e.g. single, average, centroid, complete, McQuitty or Ward), which determines whether the clusters are sufficiently similar to be linked together. Ward's method was used in this study to produce distinct clusters without the problem of excessive chaining, often experienced with other linkage methods. Ward's method is a more appropriate method than other linkage methods, such as single, average, centroid, complete or McQuitty, as it uses the analysis of variance to evaluate the distances between the clusters. As this method works by minimising the sums of squares between the clusters, it is regarded as being very efficient to discriminate between sampling sites with different species compositions (Shaw, 2003); however, it does tend to create a very large number of small clusters that may not be very easy to partition into discrete groups (Aldenderfer and Blashfield, 1984).

The second step was to select an appropriate distance measure (e.g. Euclidean, Squared Euclidian or Pearson) in order to determine how the similarities between sites should be calculated. The distance measure strongly influences the structure of the dendrogram, since some sites may be located closer to each another using one distance measure, but farther apart using another distance measure. Squared Euclidean was used as the distance measure, since it is usually linked with Ward's linkage to place progressively greater weight on sampling sites that are farther apart in terms of their species compositions. Ward's method ensures major cluster areas are widely separated on different dichotomous branches (Aldenderfer and Blashfield, 1984).

The final stage was to determine the site grouping, i.e. the classification of clusters which would identify groups of sampling sites whose species compositions shared common characteristics. This is known as cutting or partitioning the dendrogram. Cutting cannot be performed automatically by software, because it involves the researcher making subjective value judgements. As different researchers partition a dendrogram in different ways the method used in this study is defined as follows: the similarity levels (i.e. the percentages of the minimum distances between clusters relative to the maximum distances) located on the horizontal axis of the dendrogram were examined. The patterns of how the similarity levels progressively changed step by step from cluster to cluster, travelling upwards from 100% at the origin to -0% at the top of the vertical axis, were used to determine the final grouping of sites. The area near the top of the dendrogram, where the similarity levels changed most abruptly travelling from one horizontal branch to another, was explored to identify appropriate points for partitioning. The horizontal branches near the top of the dendrogram, between which the similarities appeared to change the most abruptly

from one step to the next, were identified as appropriate cut off points to partition the sampling sites into groups.

2.4.2. Multidimensional scaling

Multidimensional scaling was performed based on Principal Components Analysis (PCA) using MINITAB (version 16.1). PCA is an ordination method that aims to reveal patterns in the internal structure of the species compositions in a way that best explains the variance in the data (Shaw, 2003). PCA detects continuous variations between the sampling sites by extracting axes or components from a matrix of similarities. The species composition data were transformed into three principal components. The first component accounts for as much of the variance as possible, and each successive component in turn has the highest variance possible under the constraint that it was orthogonal to (i.e. uncorrelated with) the preceding components**.**

The three sets of principal component scores, one set of scores for each sampling site, were visually projected onto axes in three-dimensional (3D) vector space, so that the geometrical position of each sampling site relative to its fellows reflected its similarity to them. The closer together the points were in 3D vector space, then the more similar the sampling sites are in terms of their species compositions. Unlike cluster analysis, which generated a definite number of discrete groups of sampling sites, PCA assumed continuous variation between the sites (Shaw, 2003). The grouping of sampling sites identified by cluster analysis was compared to the spatial distribution of the PCA scores in 3D vector space. A high level of congruence between the outcomes of the cluster analysis and multidimensional scaling was assumed to reflect the robustness of the site classification.

2.5. Results

2.5.1. Substratum

The samples were divided into groupings according to the substratum classification made by Dingle *et al*. (1987). The West Coast of South African has a substratum made up mainly of sand and muddy-sand (Lombard et al., 2004). Over 40% of the substratum samples contained only sand, about one third consisted of muddy-sand, whereas the remainder contained various mixtures of sand and mud, with no gravel (Figure 2.2). To ensure that the trawl net would not be torn only areas where soft sediment occurred were surveyed, i.e. any areas with gravel or variations of substratum with gravel would have been avoided when sample sites were selected.

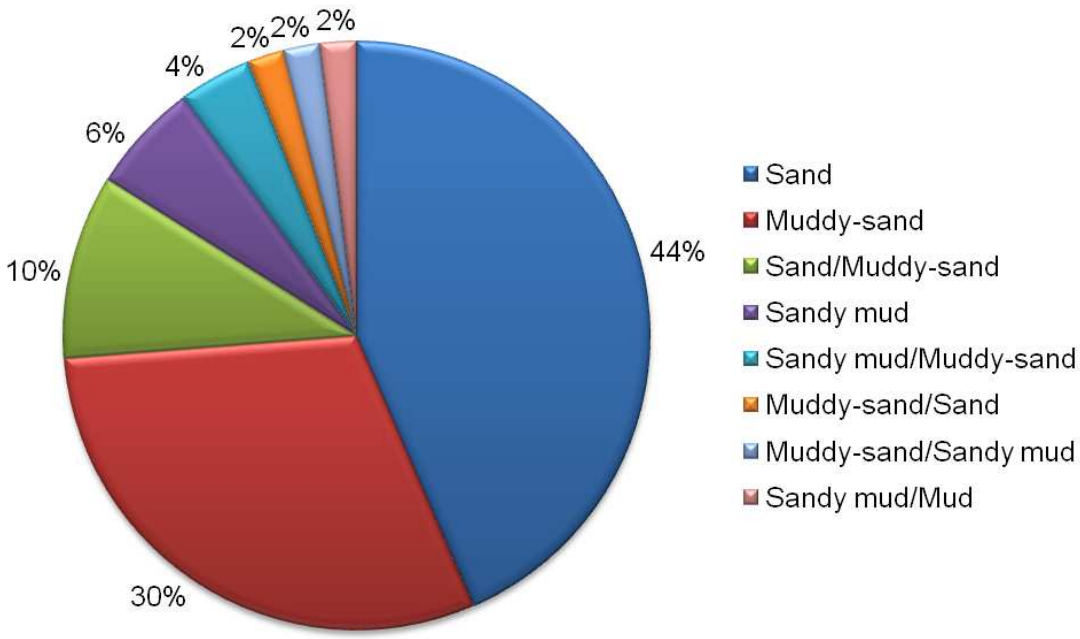


Figure 2.2. Substratum composition along the West Coast of South Africa displaying the proportion of samples in the current West Coast study that comprise each of the sediment types recognised by Dingle *et al*. (1987).

2.5.2. Depth, dissolved oxygen (DO), salinity and temperature

The physico-chemical environmental variables collected during the survey are summarized in Table 2.1. Due to the presence of the continental shelf, which ran across the survey area, the sampling sites covered a wide range of depths, ranging from 85 to 691 m (mean depth = 335.2 m, ± 149.2, S.E. = 14.99). Samples were collected from areas where the DO levels of the surrounding water ranged between 1.26 and 4.71 mg/L (mean = 3.77 mg/L, ± 0.71, S.E. = 0.07), and the samplings sites covered a narrow range of salinities, between 34.35 and 34.81 (mean = 34.59, ± 0.12, S.E. = 0.01). The water temperatures were generally low, averaging 7.7^{o}C (± 1.28, S.E. = 0.13).

Table 2.1. Summary of the environmental data collected during the Nansen West Coast survey for depth, dissolved oxygen (DO), salinity and temperature.

	Depth (m)	DO (mg/L)	Salinity	Temperature (℃)
Number of samples	99	99	99	99
Mean	335	3.77	34.57	7.7
Median	306	3.94	34.56	7.9
Minimum	85	1.26	34.35	4.9
Maximum	691	4.71	34.81	9.9
Range	606	3.45	0.45	5
Variance	22254.1	0.51	0.01	1.63
Standard deviation	149.2	0.71	0.12	1.28
Standard error	14.99	0.07	0.01	0.13

2.5.3. Faunal composition

The abundance and biomass was averaged per hectare (ha). The mean abundance of the benthic epifauna (Table 2.2) collected during the survey was 195 individuals/ha (± 438.59, S.E. = 44.08), while the biomass averaged 7 392 g/ha (± 37628.54 S.E. = 3781.21).

Table 2.2. Biomass and abundance levels of the benthic epifauna collected on the Nansen West Coast survey.

	Abundance (individuals/ha)	Biomass (g/ha)
Number of samples	99	99
Mean	195	7392
Median	55	942
Minimum	1	11
Maximum	3457	365521
Variance	1.42 x 109	1.9 x 105
Standard deviation	438.59	37628.54
Standard error (S.E.)	44.08	3781.21

A total of 103 species, from nine phyla that made up 16 classes (Table 2.3), were obtained in the 99 samples collected. The species were grouped into 16 major taxonomic groups: Anthozoa, Asteroidea, Bivalvia, Demospongiae, Echinoidea, Gastropoda, Gymnolaemata, Hexactinellida, Holothuroidea, Hydrozoa, Malacostraca, Ophiuroidea, Polychaeta, Polyplacophora, Porifera and Rhynchonellata.

Table 2.3. A list of the number of species of benthic epifauna on the Nansen West Coast survey, identified to class level.

Phylum	Class	Species
Annelida	Polychaeta	3
Arthropoda	Malacostraca	31
Brachiopoda	Rhynchonellata	1
Bryozoa	Gymnolaemata	1
Cnidaria	Anthozoa	11
Cnidaria	Hydrozoa	1
Echinodermata	Asteroidea	20
Echinodermata	Echinoidea	3
Echinodermata	Holothuroidea	2
Echinodermata	Ophiuroidea	6
Mollusca	Bivalvia	2
Mollusca	Gastropoda	16
Mollusca	Polyplacophora	1
Porifera	Hexactinellida	1
Porifera	Demospongiae	2
Porifera	Unknown Porifera	2
	Total	103

The Malacostraca and class Echinoidea were the most diverse taxonomic groups overall, with 31 species each, followed by Mollusca with 19 species. The other taxonomic groups had significantly lower species richness, with 12 species of Cnidaria, five species of Porifera (of which two species could not be identified down to class level) and three species of Polychaeta. Bryozoa and Brachiopoda were represented by only one species each.

A total of 45 314 individuals were collected, figure 2.3 shows the contributions of various taxa to the overall catch in terms of frequency (abundance). By far the most abundant species was the shallow water anemone crab *Sympagurus dimorphus*, Malacostraca (46.7%) followed by *Funchalia woodwardi*, Malacostraca (13.6%) and *Brisaster capensis* sp., Echinoidea (5.8%). The percentage composition of all the species by frequency are listed in Table 2.4.

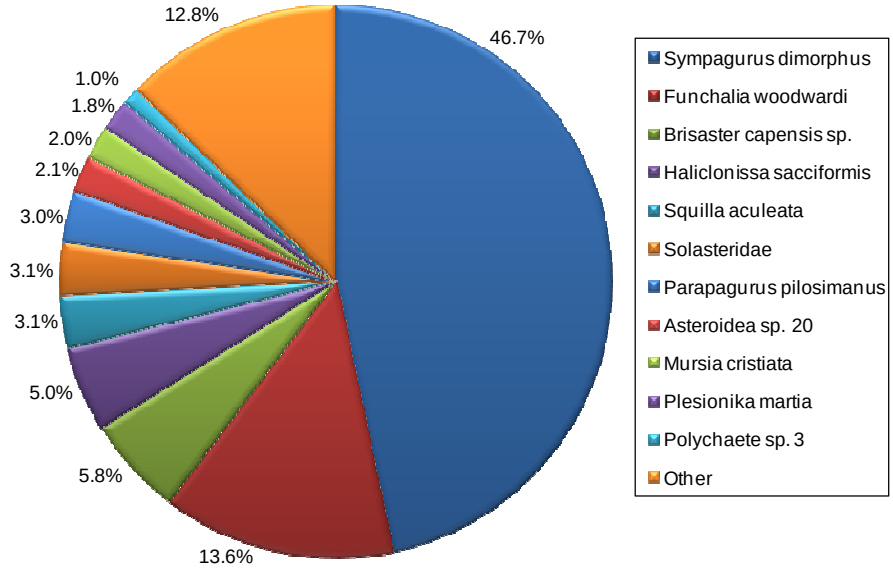


Figure 2.3. Species composition of epibenthic faunal abundance collected offshore of the West Coast of South Africa (each of the species listed under 'other' represented <1% of the total number of individuals).

Table 2.4. The species composition of the benthic epifaunal abundance collected during the Nansen West Coast survey, in total abundance, abundance per hectare and percentage frequency.

Phylum	Species	Total abundance	Mean abundance per ha	Percent (%)
Annelida	Euphrosine sp.	33	13.95	0.073
	Polychaete sp. 3	471	199.09	1.039
	Polychaete sp. 300	5	2.11	0.011
Arthropoda	Achaeopsis thomsoni	208	87.92	0.459
	Anomura sp. 300	20	8.45	0.044
	Anomura sp. 301	30	12.68	0.066
	Anomura sp. 302	5	2.11	0.011
	Aristaeomorpha foliacea	6	2.54	0.013
	Ebalia tuberosa	3	1.27	0.007
	Elthusa raynaudii	23	9.72	0.051
	Eucrate sulcatifrons	32	13.53	0.071
	Exodromidia spinosa	347	146.67	0.765
	Exodromidia spinosissima	33	13.95	0.073
	Goneplax rhomboides	8	3.38	0.018
	Homola barbata	41	17.33	0.09
	Hymenopenaeus triarthus	6	2.54	0.013
	Inachus dorsettensis	47	19.87	0.104

Phylum	Species	Total abundance	Mean abundance per ha	Percent (%)
	Merhippolyte agulhasensis	385	162.74	0.849
	Mursia cristiata	922	389.72	2.034
	Palinurus gilchristi	2	0.85	0.004
	Parapontophilus gracilis gracilis	215	90.88	0.474
	Plesionika martia	840	355.06	1.853
	Rochinia hertwigi	248	104.83	0.547
	Solenocera africana	91	38.46	0.201
	Squilla aculeata	1405	593.88	3.099
	Stereomastis	202	85.38	0.446
	Aristeus varidens	10	4.23	0.022
	Chaceon quinquedens	315	133.15	0.695
	Cymodoce alia	16	6.76	0.035
	Funchalia woodwardi	6168	2607.15	13.605
	Jasus lalandii	6	2.54	0.013
	Macropipus australis	9	3.80	0.02
	Parapagurus pilosimanus	1368	578.24	3.017
	Sympagurus dimorphus	21211	8965.68	46.786
Brachiopoda	Brachiopoda sp. 300	84	35.51	0.185
Bryozoa	Bryozoan sp. 300	6	2.54	0.013
Cnidaria	Acabaria rubra	42	17.75	0.093
	Balanophyllia	150	63.40	0.331
	Cnidaria sp. 300	40	16.99	0.089
	Cnidaria sp. 1	131	55.37	0.289
	Cnidaria sp. 2	46	19.44	0.101
	Cnidaria sp. 3	52	21.98	0.115
	Coral sp. 301	2	0.85	0.004
	Gorgonia sp. 1	9	3.80	0.02
	Gorgonia sp. 2	11	4.65	0.024
	Hydrozoa sp. 300	4	1.69	0.009
	Octocorals sp. 1	33	13.95	0.073
	Sea pen sp. 2	6	2.54	0.013
Echinodermata	Asteroidea sp. 300	4	1.69	0.009
	Asteroidea sp. 304	6	2.54	0.013
	Asteroidea sp. 306	2	0.85	0.004
	Asteroidea sp. 307	6	2.54	0.013
	Asteroidea sp. 20	965	407.90	2.129
	Asteroidea sp. 35	20	8.45	0.044
	Asteroidea sp. 303	73	30.86	0.161
	Astropecten irregularis	123	51.99	0.271

Phylum	Species	Total abundance	Mean abundance per ha	Percent (%)
	Astropecten sp. 1	6	2.54	0.013
	Astropecten sp. 2	361	152.59	0.796
	Basket star sp. 1	4	1.69	0.009
	Basket star sp. 2	5	2.11	0.011
	Basket star sp. 3	3	1.27	0.007
	Brisaster capensis sp.	2618	1106.60	5.775
	Diplopteraster multipes sp.	11	4.65	0.024
	Echinus gilchristi	75	31.70	0.165
	Holothuroidea sp. 300	17	7.19	0.037
	Holothuroidea sp. 301	4	1.69	0.009
	Luidia sarsi africana	73	30.86	0.161
	Odontaster australis	41	17.33	0.090
	Ophiuroidea sp. 500	168	71.01	0.371
	Ophiuroidea sp. 501	135	57.11	0.298
	Ophiuroidea sp. 502	20	8.45	0.044
	Persephonaster agassizi	77	32.55	0.170
	Pteraster capensis	21	8.88	0.046
	Solasteridae	1387	586.27	3.059
	Spatangus capensis	190	80.31	0.419
	Toraster tuberculatus	88	37.20	0.194
	Ceramaster patagonicus euryplax	4	1.69	0.009
	Henricia abyssalis sp.	41	17.33	0.090
	Pseudarchaster tesselatus sp.	227	95.95	0.501
Mollusca	Amalda bullioides	153	64.67	0.337
	Calliostoma scotti	28	11.84	0.062
	Conomurex decorus sp.	125	52.84	0.276
	Fasciolaria rutila	18	7.61	0.040
	Fasciolaria sp.	237	100.18	0.523
	Leptochiton sykesi	36	15.22	0.079
	Limpet sp. 300	2	0.85	0.004
	Nudibranch sp. 300	4	1.69	0.009
	Opisthobranch sp. 302	19	8.03	0.042
	Opisthobranch sp. 303	35	14.79	0.077
	Opisthobranch sp. 304	5	2.11	0.011
	Pleurobranchaea tarda	43	18.18	0.095
	Scallop sp. 300	5	2.11	0.011
	Trivia sp.	133	56.22	0.293
	Ancilla marmorata	3	1.27	0.007
	Athleta sp. 1	8	3.38	0.018
	Fusinus ocellifer	5	2.11	0.011

Phylum	Species	Total abundance	Mean abundance per ha	Percent (%)
	Galatea sp.	14	5.92	0.031
	Philine aperta	55	23.25	0.121
Porifera	Porifera sp. 2	4	1.69	0.009
	Porifera sp. 5	93	39.31	0.205
	Rosella antarctica	22	9.30	0.049
	Haliclonissa sacciformis	2252	951.90	4.967
	Mycale massa	15	6.34	0.033
	Total	45436	19205.47	100

In terms of biomass Figure 2.4 reveals that the samples were dominated by *Haliclonissa saciformis*, Demospongiae (29.4%) followed by *Palinurus gilchristi*, Malacostraca (18.7%); *Sympagurus dimorphus*, Malacostraca (11.4%) and *Funchalia woodwardi*, Malacostraca (8.3%). The percentage compositions of all species by biomass are listed in Table 2.5.

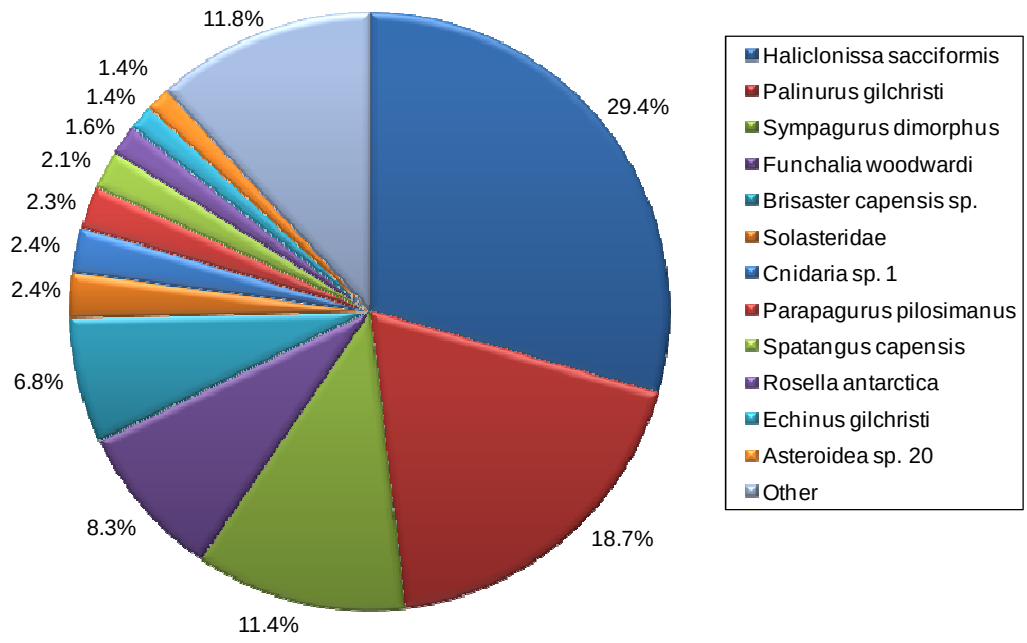


Figure 2.4. Species composition of the epibenthic faunal biomass collected offshore of the West Coast of South Africa (each of the species included in the category 'other' represented <1% of the total biomass).

Table 2.5. The species composition of benthic epifaunal biomass according to the total biomass, the biomass per hectare and percentage, collected during the Nansen West Coast survey.

Phylum	Species	Total biomass (g)	Mean biomass per hectare (g/ha)	Percent (%)
Annelida	*Euphrosine* sp.	81	34.24	0.007
	Polychaete sp. 3	3402	1437.99	0.278
	Polychaete sp. 300	653	276.02	0.053
Arthropoda	*Achaeopsis thomsoni*	1363	576.13	0.111
	Anomura sp. 300	17	7.19	0.001
	Anomura sp. 301	247	104.40	0.020
	Anomura sp. 302	75	31.70	0.006
	Aristaeomorpha foliacea	64	27.05	0.005
	Ebalia tuberosa	4	1.69	0.000
	Elthusa raynaudii	12	5.07	0.001
	Eucrate sulcatifrons	59	24.94	0.005
	Exodromidia spinosa	4657	1968.47	0.380
	Exodromidia spinosissima	143	60.44	0.012
	Goneplax rhomboides	15	6.48	0.001
	Homola barbata	53	22.58	0.004
	Hymenopenaeus triarthus	34	14.37	0.003
	Inachus dorsettensis	181	76.48	0.015
	Merhippolyte agulhasensis	1076	454.81	0.088
	Mursia cristiata	8396	3548.91	0.685
	Palinurus gilchristi	229177	96870.83	18.699
	Parapontophilus gracilis gracilis	263	111.17	0.021
	Plesionika martia	9106	3849.02	0.743
	Rochinia hertwigi	8721	3686.28	0.712
	Solenocera africana	1194	504.69	0.097
	Squilla aculeata	8231	3479.16	0.672
	Stereomastis	1282	541.89	0.105
	Aristeus varidens	145	61.29	0.012
	Chaceon quinquedens	9107	3849.44	0.743
	Cymodoce alia	25	10.69	0.002
	Funchalia woodwardi	101586	42939.39	8.288
	Jasus lalandii	432	182.60	0.035
	Macropipus australis	294	124.27	0.024
	Parapagurus pilosimanus	28689	12126.41	2.341
	Sympagurus dimorphus	140069	59205.66	11.428
Brachiopoda	Mollusca sp. 300	1069	451.86	0.087
Bryozoa	Bryozoan sp. 300	10	4.23	0.001

Phylum	Species	Total biomass (g)	Mean biomass per hectare (g/ha)	Percent (%)
Cnidaria	*Acabaria rubra*	1136	480.18	0.093
	Balanophyllia	2503	1057.99	0.204
	Cnidaria sp. 300	330	139.49	0.027
	Cnidaria sp. 1	29117	12307.46	2.376
	Cnidaria sp. 2	4494	1899.57	0.367
	Cnidaria sp. 3	6226	2631.67	0.508
	Coral sp. 301	350	147.94	0.029
	Gorgonia sp. 1	170	71.86	0.014
	Gorgonia sp. 2	36	15.22	0.003
	Hydrozoa sp. 300	31	13.10	0.003
	Octocoral sp. 1	444	187.67	0.036
	Sea pen sp. 2	642	271.37	0.052
Echinoderm ata	Asteroidea sp. 300	692	292.50	0.056
	Asteroidea sp. 304	24	10.14	0.002
	Asteroidea sp. 306	251	106.10	0.02
	Asteroidea sp. 307	83	35.08	0.007
	Asteroidea sp. 20	16362.9	6916.43	1.335
	Asteroidea sp. 35	473	199.93	0.039
	Asteroidea sp.303	730	308.56	0.060
	Astropecten irregularis	2361.762	998.29	0.193
	Astropecten sp. 1	66	27.90	0.005
	Astropecten sp. 2	2682	1133.65	0.219
	Basket star sp. 1	130	54.95	0.011
	Basket star sp. 2	293	123.85	0.024
	Basket star sp. 3	5	2.11	0.000
	Brisaster capensis sp.	83786.714	35415.81	6.836
	Diplopteraster multipes sp.	3529	1491.67	0.288
	Echinus gilchristi	16711	7063.57	1.363
	Holothuroidea sp. 300	15	6.34	0.001
	Holothuroidea sp. 301	2773	1172.12	0.226
	Luidia sarsi africana	9537.31	4031.33	0.778
	Odontaster australis	2341.929	989.91	0.191
	Ophiuroidea sp. 500	563	237.97	0.046
	Ophiuroidea sp. 501	568.767	240.41	0.046
	Ophiuroidea sp. 502	114	48.19	0.009
	Persephonaster agassizi	5136.5	2171.15	0.419
	Pteraster capensis	491	207.54	0.040
	Solasteridae	29661	12537.41	2.420
	Spatangus capensis	25701.429	10863.74	2.097
	Toraster tuberculatus	7115.571	3007.68	0.581

Phylum	Species	Total biomass (g)	Mean biomass per hectare (g/ha)	Percent (%)
Echinoderm ata	*Ceramaster patagonicus euryplax*	94	39.73	0.008
	Henricia abyssalis sp.	160	67.63	0.013
	Pseudarchaster tesselatus sp.	4094.333	1730.63	0.334
Mollusca	*Amalda bullioides*	943	398.60	0.077
	Calliostoma scotti	78	32.97	0.006
	Conomurex decorus sp.	4252.667	1797.56	0.347
	Fasciolaria rutila	1153	487.36	0.094
	Fasciolaria sp.	10885.333	4601.12	0.888
	Leptochiton sykesi	33	13.95	0.003
	Limpet sp. 300	2	0.85	0.000
	Nudibranch sp. 300	13	5.49	0.001
	Opisthobranch sp. 302	97	41.00	0.008
	Opisthobranch sp. 303	1248	527.52	0.102
	Opisthobranch sp. 304	130	54.95	0.011
	Pleurobranchaea tarda	1995.71	843.57	0.163
	Scallop sp. 300	22	9.30	0.002
	Trivia sp.	133	56.22	0.011
	Ancilla marmorata	26	10.99	0.002
	Athleta sp. 1	69.333	29.31	0.006
	Fusinus ocellifer	81	34.24	0.007
	Galatea sp.	58	24.52	0.005
	Philine aperta	172	72.70	0.014
Porifera	Porifera sp. 2	71	30.01	0.006
	Porifera sp. 5	1117	472.14	0.091
	Rosella antarctica	19966.429	8439.61	1.629
	Haliclonissa sacciformis	359979	152159.52	29.371
	Mycale massa	1156	488.63	0.094
	Total	1225640.1	518065.81	100

In order to examine depth related changes in catch composition, samples were grouped in 100 m depth intervals defined *a priori*. No samples were collected in water shallower than 50 m. In Table 2.6 species richness per sample (trawl) is displayed. Asteroidea and Malacostraca were the two classes that were the most species richness in all depth intervals. The 0 - 99 m depth interval was the most species rich, however only one sample was taken at this depth. The second most species rich depth interval was 300 - 399 m, followed by the 400 - 499 m interval. In the deepest depths sampled, 600 - 699 m, only Anthozoa, Asteroidea, Gastropoda, Holothuroidea and Malacostraca were present.

Table 2.6. Species richness per trawl for each class sampled in each depth interval along the West Coast during the Nansen West Coast survey.

Depth (m)	Anthozoa	Asteroidea	Bivalvia	Demospongiae	Echinoidea	Gastropoda
0-99	-	4.00	-	-	1.00	1.00
100-199	0.29	0.76	-	0.10	0.14	0.52
200-299	0.41	0.59	0.04	0.07	0.11	0.52
300-399	0.53	1.12	0.06	0.06	0.18	0.76
400-499	0.24	1.06	0.12	-	0.12	0.41
500-599	0.25	0.58	0.08	-	-	0.17
600-699	0.25	0.50	-	-	-	0.25
	Gymnolaemata	Hexactinellida	Holothuroidea	Hydrozoa	Malacostraca	Ophiuroidea
0-99	-	1.00	-	-	3.00	1.00
100-199	0.05	-	-	-	0.86	0.14
200-299	-	0.04	0.04	-	0.67	0.22
300-399	-	0.06	0.06	0.06	1.24	0.24
400-499	-	0.06	-	-	1.29	0.24
500-599	-	0.00	0.08	-	0.92	-
600-699	-	-	0.25	-	1.25	-
	Polychaeta	Polyplacophora	Porifera	Rhynchonellata	Species per sample	
0-99	-	-	-	-	11	
100-199	0.05	-	0.05	0.05	3	
200-299	0.07	0.04	0.07	0.04	2.93	
300-399	0.12	0.06	0.06	0.06	4.65	
400-499	0.12	-	-	0.06	3.71	
500-599	0.08	-	-	-	2.17	
600-699	-	-	-	-	2.5	

Table 2.7 shows the taxonomic breakdown of the fauna in each depth interval in terms of biomass per sample. The highest values were recorded in the 100 - 199 m depth interval, and decreases in deeper intervals, with a slight increase in the 400 - 499 and 600 - 699 m depth interval. Echinoidea dominated the

shallow depth intervals (0 - 99 m) and Demospongiae the 300 - 399 m depth interval. Malacostraca were found to dominate the remaining depth intervals. The taxonomic groups showing the second highest biomass for each depth interval were move variable. Hexactinellida had the second highest biomass value in the 0 - 99 m depth interval, Demospongiae at 100 - 199 m and Echinoidea in the 200 - 299 m depth interval. Asteroidea were second ranked group at 300 - 399 m, 400 - 499 m and 600 - 699 m depth intervals, and Anthozoa at 500 - 599 m depth interval.

Table 2.7. Biomass per trawl for each Class sampled in each depth interval along the West Coast during the Nansen West Coast survey. The number of samples taken in each depth interval is given in brackets.

Depth interval	Anthozoa	Asteroidea	Bivalvia	Demospongiae	Echinoidea	Gastropoda
0-99 (1)	-	260.0	-	-	3638.0	118.0
100-199 (21)	270.4	546.3	-	15087.5	4129.7	369.4
200-299 (27)	175.5	553.8	0.3	210.7	1164.0	161.9
300-399 (17)	976.6	1098.8	0.4	2271.1	246.6	278.2
400-499 (17)	829.2	2127.5	2.5	-	12.7	176.5
500-599 (12)	340.4	339.4	2.0	-	-	103.1
600-699 (4)	62.0	70.3	-	-	-	16.0
	Gymnolaemata	Hexactinellida	Holothuroidea	Hydrozoa	Malacostraca	Ophiuroidea
0-99	-	471.0	-	-	119.0	33.0
100-199	0.5	-	-	-	15674.1	6.9
200-299	-	82.1	0.4	-	2039.1	27.9
300-399	-	214.3	0.3	1.8	2148.4	26.8
400-499	-	802.1	-	-	5817.5	17.0
500-599	-	-	217.7	-	1477.0	-
600-699	-	-	40.3	-	4319.5	-
	Polyplacophora	Porifera	Rhynchonellata	Total biomass per trawl		
0-99	-	-	-	4639.0		
100-199	-	52.5	3.6	36170.7		
200-299	0.3	1.7	36.4	4456.4		
300-399	1.4	2.3	0.5	7460.5		
400-499	-	-	0.1	9793.8		
500-599	-	-	-	2481.3		
600-699	-	-	-	4508.0		

In terms of abundance per trawl (Table 2.8), the 200 - 299 m depth interval displayed the highest abundance values, followed closely by the 100 - 199 m and 400 - 499 m depth intervals. Malacostraca dominated the abundance values at all the depth intervals, except 0 - 99 m where Asteroidea displayed the highest abundance. Echinoidea displayed the second highest abundance values in the 0 - 99 m, 100 -

199 m and Demospongiae in the 200 -299 m depth interval. The second most abundant class in the remaining depth intervals was Asteroidea.

Table 2.8. Abundance per trawl for each class sampled in each depth interval along the West Coast during the Nansen West Coast survey. The number of samples in each depth interval is given in brackets.

Depth interval	Anthozoa	Asteroidea	Bivalvia	Demospongiae	Echinoidea	Gastropoda
0-99 (1)	-	30.0	-	-	17.0	13.0
100-199 (21)	2.2	15.4	-	18.2	108.2	8.8
200-299 (27)	3.0	18.8	0.1	50.6	20.7	5.0
300-399 (17)	17.3	39.2	0.1	30.4	1.7	15.5
400-499 (17)	4.5	102.6	0.8	-	0.4	9.5
500-599 (12)	1.9	19.8	0.2	-	-	1.4
600-699 (4)	0.3	4.8	-	-	-	0.3
	Gymnolaemata	Hexactinellida	Holothuroidea	Hydrozoa	Malacostraca	Ophiuroidea
0-99	-	2.0	-	-	13.0	3.0
100-199	0.3	-	-	-	394.4	1.6
200-299	-	0.1	0.6	-	504.6	7.7
300-399	-	0.9	0.1	0.2	147.2	5.0
400-499	-	0.1	-	-	398.3	0.2
500-599	-	-	0.3	-	144.2	-
600-699	-	-	0.3	-	346.5	-
	Polychaeta	Polyplacophora	Porifera	Rhynchonellata	Total abundance per trawl	
0-99	-	-	-	-	78.0	
100-199	0.5	-	4.0	1.8	555.4	
200-299	0.2	0.3	0.3	1.6	613.7	
300-399	24.6	1.6	0.2	0.1	284.1	
400-499	4.2	-	-	0.2	520.7	
500-599	0.3	-	-	-	167.9	
600-699	-	-	-	-	352.0	

2.5.4. Cluster analysis

Hierarchical cluster analysis was used to classify the sampling sites into groups according to the similarities in their species compositions. The cluster analysis produced distinct subsets within the data (Figure 2.5). The dendrogram was cut at the chosen points to generate the major dichotomous branches, identified visually as black lines. The black lines represented the lowest levels of similarity which could, according to the judgment of the researcher, be used to separate the clusters of sampling sites into distinct groups. For convenience, each group of sampling sites was visually identified in the dendrogram using a different colour.

The 99 sampling sites on the West Coast were clustered into six major groups: coloured red (13 sites), green (79 sites), blue (2 sites), pink (2 sites), orange (1 site) and purple (2 sites) (Figure 2.5). It was not possible to label the sites on the horizontal axis due to lack of space, therefore the dendrogram was decomposed by cluster groups for this purpose. The dendrogram was structured with group 1 (red) located on the left hand side, a large group 2 (green) at the centre, and several smaller groups containing one or two sites on the right hand side, those on the far right being the most dissimilar groups.

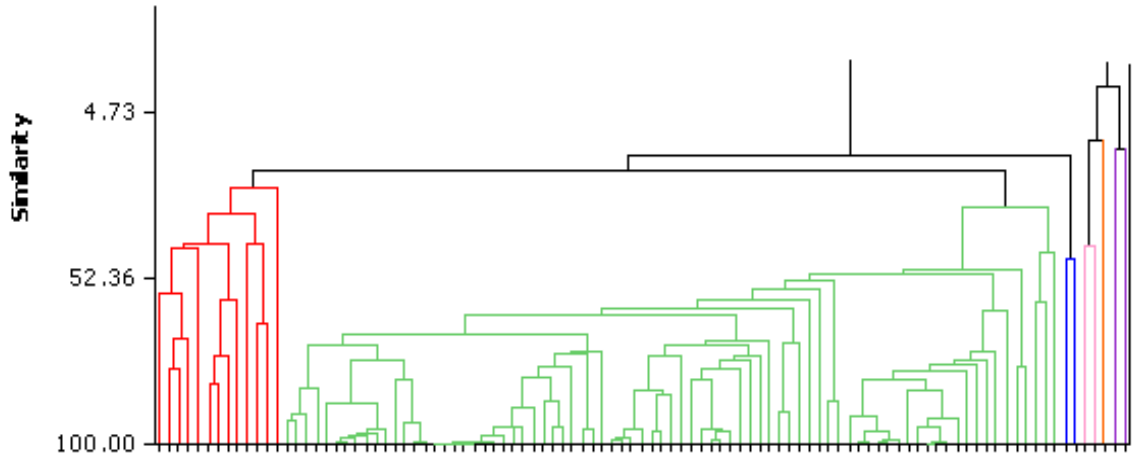


Figure 2.5. Hierarchical cluster analysis of 99 sites that were sampled during the Nansen West Coast survey.

2.5.5. Multidimensional scaling

The first three principal component scores (PCA1, PCA2, and PCA3) explained 43.5% of the species compositions. When distributed in a 3D scatterplot (Figure 2.6) the PCA scores for each site group classified using hierarchical cluster analysis were not all located in separate areas of vector space. Group 1 (red circles) appeared contiguous with group 2 (green squares), while group 5 (orange triangle) and group 4 (pink triangle) were closely juxtaposed.

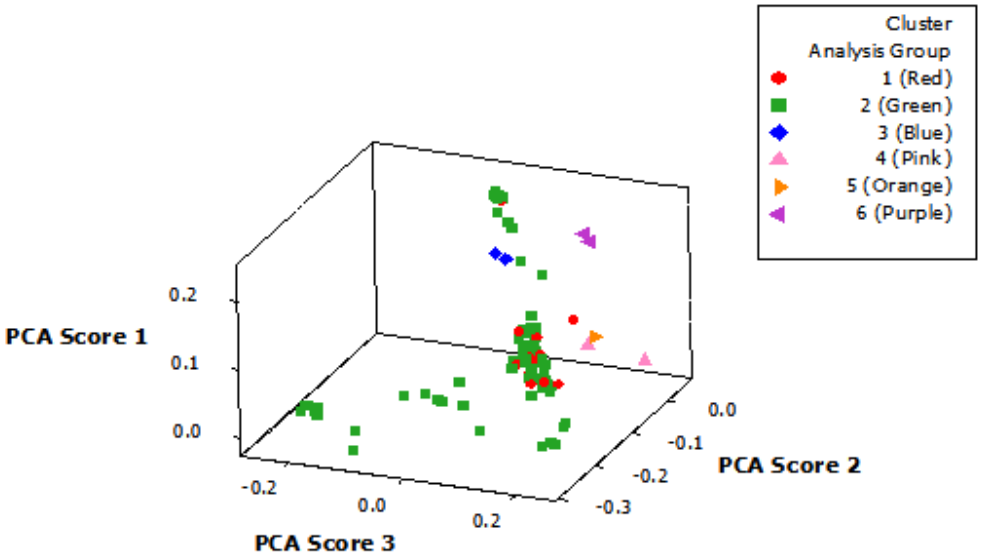


Figure 2.6. First three principal component (PC) scores for the 99 sites sampled during the Nansen West Coast survey, based on similarities by percentage species composition.

2.5.6. Comparison of the species compositions at the six site groups

The percentage species composition data for the Nansen Survey were partitioned into the six site groups identified by cluster analysis. The percentage species compositions within each of the six groups are compared in Table 2.9. The six groups of sampling sites were characterised by different species compositions by frequency. The dominant species (each contributing >5%) in group 1, in order of relative abundance, were *Mursia cristiata*, Malacostraca (11.2%); *Rochinia hertwigi*, Malacostraca (9.7%); Cnidaria sp. 1 (8.7%); Octocoral sp. 1 (6.9%); *Merhippolyte agulhasensis*, Malacostraca (6.7%) and Cnidaria sp. 3 (5.2%); together contributing almost half of the invertebrates collected during the survey.

In group 2 four species represented approximately one quarter of the invertebrates counted, namely *Sympagurus dimorphus*, Malacostraca (5.3%); *Funchalia woodwardi*, Malacostraca (5.3%); *Parapaguris pilosimanus*, Malacostraca (5.2%); *Briaster capensis*, Echinoidea (5.2%) and Porifera sp. 5 (5.1%). Group 3 was dominated by three species, *Haliclonissa sacciformis*, Demospongiae (38.6%); *Astropecten irregularis*, Asteroidea (13.6%) and *Spatangus capensis*, Echinoidea (10.9%).

Six species represented over half of the invertebrates counted in group 4, namely Balanophyllia sp., Anthozoa (14.4%); *Sympagurus dimorphus*, Malacostraca (9.8%); *Parapagurus pilosimanus*, Malacostraca (5.2%); *Achaeopsis thomsoni*, Malacostraca (5.0%); *Asteroidea* sp. 20, Asteroidea (10.8%); and *Haliclonissa sacciformis*, Demospongiae (7.4%). In group 5, *Asteroidea* sp. 20, Asteroidea (16.3%); Ophiuroidea sp. 500, Ophiuroidea (11.4%); *Spatangus patengus*, Echinoidea (5.4%) and *Haliclonissa sacciformis*, Demospongiae (5.4%) collectively contributed over a third of the number of invertebrates

counted. Over half of the invertebrates collected at group 6 consisted of Ophiuroidea sp. 500, Echinodermata (34.1%); *Mycale massa*, Demospongiae (12.6%) and *Achaeopsis thomsoni*, Malacostraca (9.2%).

These groups were then named according to the most abundant species present. Group 1 became the *Mursia* community, group 2 the *Sympaturus* community, group 3 the *Haliclonissa* community, group 4 the *Balanophyllia* community, group 5 the Asteroidea community, and group 6 the Ophiuroidea community.

Table 2.9. Percentage species compositions (%) of the benthic epifauna at the six site groups differentiated by the cluster analysis.

		Site Group					
Phylum	Species	1	2	3	4	5	6
Annelida	*Euphrosine* sp.	4.3	<0.1	-	-	-	-
	Polychaeta sp. 3	<0.1	3.6	-	-	-	5.3
	Polychaete sp. 300	-	<0.1	-	-	-	2
Arthropoda	*Achaeopsis thomsoni*	2.6	0.4	-	5	3	9.2
	Anomura sp. 300	<0.1	-	1.7	-	-	-
	Anomura sp. 301	<0.1	0.1	-	3.7	-	-
	Anomura sp. 302	0.5	<0.1	-	-	-	-
	Aristaeomorpha foliacea	-	<0.1	-	-	-	-
	Ebalia tuberosa	-	<0.1	-	0.2	-	-
	Elthusa raynaudii	<0.1	0.2	-	-	1.8	-
	Eucrate sulcatifrons	0.6	<0.1	-	0.6	0.6	-
	Exodromidia spinosa	1	3.4	0.3	0.6	-	-
	Exodromidia spinosissima	0.2	0.1	-	3.6	5.4	-
	Goneplax rhomboides	-	0.1	-	-	-	-
	Homola barbata	<0.1	0.1	-	2.7	4.2	2.6
	Hymenopenaeus triarthus	<0.1	<0.1	-	-	-	-
	Inachus dorsettensis	-	0.1	6.7	-	-	-
	Merhippolyte agulhasensis	6.7	4.3	-	-	-	-
	Mursia cristiata	11.2	1.2	4.9	2.6	-	-
	Palinurus gilchristi	-	<0.1	-	-	-	-
	Parapontophilus gracilis gracilis	2.5	-	-	-	-	-
	Plesionika martia	<0.1	4.7	-	-	-	-
	Rochinia hertwigi	9.7	0.6	-	-	0.6	-
	Solenocera africana	-	3.7	-	-	-	-
	Stereomastis	<0.1	4.6	-	-	-	-
	Aristeus varidens	-	0.1	-	-	-	-

		Site Group					
Phylum	Species	1	2	3	4	5	6
	Chaceon quinquedens	-	3.1	-	-	-	-
	Funchalia woodwardi	-	5.3	-	-	-	-
	Jasus lalandii	<0.1	0.1	-	-	-	-
`	*Macropipus australis*	<0.1	0.8	-	-	-	-
	Parapagurus pilosimanus	2	5.2	-	8.7	-	-
	Sympagurus dimorphus	0.7	5.3	-	9.8	2.4	-
Brachiopoda	Mollusca sp. 300	-	2.1	-	-	-	-
Bryozoa	Bryozoan sp. 300	-	<0.1	0.5	-	-	-
Cnidaria	*Acabaria rubra*	<0.1	0.1	0.5	2.6	0.6	-
	Balanophyllia sp.	0.1	0.2	0.5	14.4	0.6	1.3
	Cnidaria sp. 300	0.9	0.5	-	-	1.8	-
	Cnidaria sp. 1	8.7	0.6	-	-	-	-
	Cnidaria sp. 2	1.5	0.2	-	-	-	-
	Cnidaria sp. 3	5.2	0.2	-	-	0.6	3.9
	Coral sp. 301	-	<0.1	-	-	-	-
	Gorgonia sp. 1	<0.1	-	-	-	-	1.3
	Gorgonia sp. 2	-	0.1	-	-	-	1
	Hydrozoa sp. 300	<0.1	-	-	0.2	-	-
	Octocorals sp. 1	6.9	0.2	-	-	1.8	-
	Sea pen sp. 2	-	0.1	-	-	1.2	-
	Asteroidea sp. 304	<0.1	<0.1	-	0.2	-	-
	Asteroidea sp. 306	-	0.2	-	-	-	-
	Asteroidea sp. 307	-	<0.1	-	-	-	-
	Asteroidea sp. 20	1	2.5	-	10.8	16.3	1
	Asteroidea sp. 35	<0.1	<0.1	-	0.1	0.6	2
	Asteroidea sp.303	1.4	0.3	-	1.2	5.4	-
	Astropecten irregularis	<0.1	1.1	13.6	-	0.6	-

		Site Group					
Phylum	Species	1	2	3	4	5	6
	Astropecten sp. 1	<0.1	0.1	-	-	-	-
	Astropecten sp. 2	7.7	1.4	-	5.7	2.4	-
	Basket star sp. 2	-	<0.1	-	-	-	2.6
	Basket star sp. 3	0.2	-	-	-	0.6	-
	Brisaster capensis sp.	0.4	5.2	-	-	3	1
	Diplopteraster multipes sp.	0.2	0.1	-	-	-	-
	Echinus gilchristi	0.6	0.5	2.3	0.1	-	-
	Holothuroidea sp. 300	-	0.1	-	-	4.2	-
	Holothuroidea sp. 301	-	<0.1	-	-	-	-
	Luidia sarsi africana	0.2	0.6	1.3	1.9	1.2	-
	Odontaster australis	<0.1	0.2	5	-	-	-
	Ophiuroidea sp. 500	<0.1	0.8	-	0.5	11.4	34.1
	Ophiuroidea sp. 501	0.5	2	-	1.3	1.2	1
	Ophiuroidea sp. 502	-	0.2	-	0.2	3	-
	Persephonaster agassizi	2.2	1.1	-	0.9	-	-
	Pteraster capensis	0.4	0.1	0.1	1.1	0.6	1
	Solasteridae	1.8	4.9	-	0.7	-	2.6
	Toraster tuberculatus	1.7	0.6	0.7	0.2	-	-
	Ceramaster patagonicus euryplax	0.3	<0.1	-	-	-	-
	Henricia abyssalis sp.	0.4	0.1	-	0.1	0.6	1.3
	Pseudarchaster tesselatus sp.	0.5	1.6	-	1.1	1.2	-
Mollusca	*Amalda bullioides*	1.2	0.5	-	1.3	0.6	-
	Calliostoma scotti	-	0.1	-	-	2.4	2.3
	Conomurex decorus sp.	1.8	0.3	-	0.8	-	1
	Fasciolaria rutila	0.5	<0.1	-	1.1	-	-
	Fasciolaria sp.	4.6	0.9	-	0.8	0.6	-
	Leptochiton sykesi	-	0.1	-	-	-	-

		Site Group					
Phylum	Species	1	2	3	4	5	6
	Limpet sp. 300	-	<0.1	-	-	-	-
	Nudibranch sp. 300	-	<0.1	-	-	1.2	-
	Opisthobranch sp. 302	-	0.1	-	0.8	3.6	1
	Opisthobranch sp. 304	-	0.1	-	-	-	-
	Pleurobranchaea tarda	3.2	<0.1	8.3	-	-	-
	Scallop sp. 300	-	<0.1	-	0.9	1.2	-
	Trivia	<0.1	0.1	0.2	-	2.4	-
	Ancilla marmorata	-	<0.1	-	1.8	-	-
	Athleta sp. 1	<0.1	<0.1	-	-	-	-
	Fusinus ocellifer	-	0.4	-	0.2	-	-
	Galatea sp.	<0.1	<0.1	-	-	-	-
	Philine aperta	4.1	-	-	-	-	-
Porifera	Porifera sp. 2	-	<0.1	-	-	-	1.3
	Rosella antarctica	1.3	1.1	1.3	0.7	-	-
	Haliclonissa sacciformis	<0.1	4.8	38.6	7.4	5.4	-
	Mycale massa	-	<0.1	-	-	-	12.6

2.5.7. Relationships between species richness and environmental variables

It was not possible to perform an ANOVA to compare the mean species richness and the mean values of the physico-chemical variables across the groups of sampling sites clustered by similar species compositions. This was due to the strong violations of the theoretical assumptions of an ANOVA, including the large difference in the number of sampling sites per group, two groups having only one site, deviations from normality, and the highly unequal variances across the groups. Box plots were constructed to visualize any systematic relationships between the groups of sites and the species diversity indices. No relationships were evident.

2.6. Discussion

2.6.1. Faunal composition

The present study found Malacostraca (Crustacea) to be the dominant group in terms of the number of species (31 species in total, from 99 trawls), averaging 4 species per trawl. The second most species rich group were the Echinodermata (31 species in total; from 99 samples), averaging 3.8 species per trawl, while Mollusca had the third highest species richness with an average of 1.8 species per sample (19 species in total, from 99 samples). The presence of a limited number of dominant components is common in deep sea benthic communities and is explained in response to perturbation (Thistle *et al.*, 1985; Smith *et al.*, 1986). For example, strong bottom currents create episodic events, i.e. sediment-transporting disturbances (Thistle *et al.*, 1985), which lead to the limited number of dominant species capable of colonising the area.

During this survey Malacostraca (Crustacea) were also the most abundant group (75%), while the major contributors to the remainder of the total community were made up of Asteroidea, Echinoidea, Demospongiae and Gastropoda (Figure 2.4). On the West Coast, Malacostraca and Demospongiae were the major contributors to biomass (75% combined), with the third largest contributor to biomass being Echinoidea. In this study Echinodermata (consisting of Asteroidea, Echinoidea, Holothuroidea and Ophiuroidea) contributed 17.7% to the total biomass (Figure 2.5 and Table 2.5). The dominance of Crustacea in the benthic samples are similar to patterns found in surveys off Western Australia (Poore et al., 2008) .

This study was not comparable to other studies undertaken in the same area, as these studies were either taxon specific (Melville-Smith, 1988; Beyers, 1994; Hiller, 1994; Turpie *et al*., 2000), or used very different sampling methods, such as grabs, and were restricted to specific sites (Field, 1971; Christie, 1974). It should be noted that, when attempting to compare this current study's data to other studies, the Echinodermata in this study were divided into four classes: Asteroidea, Echinoidea, Holothuroidea and Ophiuroidea; while the Porifera into two classes: Demospongiae and (unknown) Porifera; the Mollusca

into three classes: Gastropoda, Bivalvia and Polyplacophora; and the Cnidaria into two classes: Anthozoa and Hydrozoa.

2.6.2. Environmental patterns

In this study, the macrofaunal communities along the West Coast of South Africa appeared spatially heterogeneous in terms of structure and distribution. De Léo and Pires-Vanin (2006) found that a combination of sediment type and depth accounted for the macrofaunal distribution patterns observed on the Brazilian shelf, while Escaravage *et al.* (2009) studied the North Sea, Adriatic and Aegean Seas and found a close relationship between depth and fraction of surface primary production that reaches the seafloor. In addition to depth and sediment type, primary productivity could be important in this study, as the West Coast of South Africa is a major upwelling site with high primary productivity in the surface waters (Shannon, 1985). Le Loeuff and Von Cosel (1998) also found that faunal richness was higher at an upwelling site along the Atlantic coast; however, Cleary *et al.* (2005) found, at Indonesia's Spermonde Archipelago, that even when upwelling was considered, depth was the most important explanatory variable for community composition. In various regions of the world, depth has been shown to affect the spatial variation in benthic communities (e.g. Christie, 1974 [small scale study]; Villanueva, 1992; Cartes and Sardà, 1993; Stefanescu *et al.*, 1993; Moranta *et al.*, 1998; Maynou and Cartes, 2000; Quetglas *et al.*, 2000; Jones *et al.*, 2003; Madurell *et al.*, 2004), however, during this study there were no apparent relationships with the environmental variables or depth. It is, however, possible that further structured sampling in each depth range and sediment type will reveal a relationship between community structure and environmental variables. Satellite data could also be averaged across years or months to provide indices that might prove more reliable as predictors of species richness than spot measures as the benthic fauna are integrating the environmental signal.

Various studies have also found that sediment type determines the distribution of benthic species assemblages (Carney, 2005; De Léo and Pires-Vanin, 2006; Escaravage *et al.*, 2009). This study, however, did not show sediment type to be a variable that affects the distribution pattern of the benthic fauna, as seen in Figure 2.7, which shows the current communities superimposed over a sediment map of South Africa. The map, however, should be interpreted with caution, as the sediment data date back to 1987 and may have changed in the last 22 years, due to the dynamic nature of the upwelling region in which the current survey was conducted. Furthermore, these sediment data (Dingle *et al*., 1987) were interpolated from a series of samples and there were almost certainly reefs and pockets of different habitat types within these broad regions. As a result, further investigations of sediment type as a variable are required and will, in all likelihood, have a determining effect on the distribution patterns of the benthic invertebrates on the West Coast of South Africa.

The highest number of species (21 species per trawl) was recorded in the 300 - 399 m depth interval, while the lowest numbers were recorded in the 600 - 699 m (5 species per trawl) and 500 - 599 m (7

species per trawl) depth intervals. Flach and De Bruin (1999) conducted a study across the continental slope in the North East Atlantic and found that the least number of species occurred in the shallower depths. With regards to the composition of benthic communities at different depths Gage (2001) noted that the Atlantic North and West of coasts of Scotland displayed a species number composition that was broadly similar at similar depths. This current study, however, found that a combination of Asteroidea, Gastropoda and Malacostraca species dominated the shallower regions, while a combination of Asteroidea and Malacostraca species were most abundant in the deeper regions. In terms of biomass, the shallow regions were dominated by Demospongiae and Malacostraca, while the deeper regions were dominated by Malacostraca and Anthozoa. Echinodermata, consisting of Asteroidea, Echinoidea, Holothuroidea and Ophiuriodea, displayed the highest biomass values in the 0 - 99 m depth interval, as well as the second highest biomass in the 200 - 299, 400 - 499, 500 – 599 and 600 - 699 m depth intervals (Table 2.6). Similarly, in the Balearic Basin the Echinoderm species were responsible for peaks in biomass (Cartes *et al.*, 2009). In Walvis Bay, off the coast of Namibia, species diversity at depths from 100 - 2140 m have been shown to decline with reduced oxygen content in the bottom waters (Sanders, 1969). The reduced oxygen is a result of high oxygen demand in an area of upwelling and high surface productivity. Thus, the dominance by a few species in specific depth intervals may be explained by either a tolerance for low oxygen conditions, or an ability to rapidly increase in density in response to increased food.

The highest abundance levels were recorded on the continental margin and upper continental slope during this study. The highest biomass and abundance values in this study were recorded in the 100 - 199 m and 200 - 299 m depth intervals, respectively (Table 2.7). The lowest biomass values were recorded in the 500 - 599 m depth interval, while the lowest abundance values were in the 0 - 99 m and 500 - 599 m depth intervals (Table 2.8). In general, studies have attributed the low species abundance in the shallow regions to pollution and high eutrophication (Carballo *et al.*, 1996; Langer and Lipps, 2003; Du Châtelet *et al.*, 2004). Escobar-Briones *et al.* (2008), however, attributed the diminishing trend of megacrustaceans with depth, observed in the Gulf of Mexico, to the high trophic position of certain groups of crustaceans, and to the energy limitation at depth. For example, deeper regions tend to exhibit lower abundances and biomass, as seen in the current study, with the exponential decline in biomass with increasing depth linked to the dependence on surface-derived food (Belyaev, 1966; Filatova, 1982).

Previous worldwide studies demonstrated that general benthic macrofaunal distribution patterns exhibit a pronounced depth dependency (Pires, 1992; Long *et al.*, 1995; Escobar-Briones and Soto, 1997; Fariña *et al.*, 1997; Pires-Vanin, 2001; De Léo and Pires-Vanin, 2006). The depth dependency of certain benthic macrofauna may be related to light penetration (Cleary *et al.*, 2005). For example, as depth increases light penetration is reduced, thus light penetration is important in determining distributional patterns of benthic macrofauna. In addition, differences in nutrient availability and fluvial influx may also play an important role in benthic species distributions, as they too can influence light penetration (Cleary *et al.*,

2005). The general distributional patterns of the benthic macrofauna obtained for the West Coast of South Africa (Figure 2.7) did not exhibit a depth dependency. Cleary *et al.* (2005) found, at the Indonesia's Spermonde Archipelago, that depth was important for some taxa, such as sponges, while for others, such as sea urchins, depth was relatively unimportant. The relative unimportance of depth in the current study could be due to the sample size as it is possible that a greater number of samples on a finer scale will reveal more pronounced environmental relationships. Also the average oceanographic properties are strongly correlated with depth and it is therefore difficult to disentangle the drivers (Pers. Comm. P. Dunstan)

2.6.3. Biogeography

The cluster analysis revealed several communities (groups) each defined by particular species. Group 1 was characterised by the crab *Mursia cristiata*, distributed mainly on the continental shelf of South Africa's West coastline. The largest group, group 2, was dominated by the shallow water anemone crab, *Sympagurus dimorphus*, with a very broad distribution range. The group with the shallowest distribution, <100 m depth, was group 3, which only occurred to the south of the sampling region (Figure 2.7) and was characterised by the Porifera species, *Haliclonissa sacciformis*. Group 4 was dominated by a Cnidaria species, *Balanophyllia* sp. This group occurred north-west of the sampling region, on the continental shelf, close to the 500 m isobath. Asteroidea sp. 20 characterised group 5. It should be noted, however, that group 5 only consisted of one sample. The final group, group 6, mainly consisted of the brittle star, Ophiuriodea sp. 500. This brittle star community was found to the north of the sampling site and interestingly only occurred in muddy-sand, even though no direct link between substratum and species distribution could be found.

Lombard *et al.* (2004) described three bioregions along the West Coast of South Africa: the Namaqua Bioregion, the South-Western Cape Bioregion, and the Atlantic Offshore Bioregion (assumed to extend to the edge of the continental shelf). These biozones were then further divided into five depth strata. Only three bioregions were delimited, as Lombard *et al.* (2004) assumed that the marine biota became more homogeneous from the intertidal to the abyssal zones, based on water temperature. However, this current study indicates no basis for a division between the Namaqua and South-Western Cape Bioregions, and also no division due to depth. The current study's results show two large communities and four patchy smaller groups/communities, thus implying that the bioregions delimited by Lombard *et al.* (2004) need to be revisited.

This study has shown that the fauna is heterogeneous and diverse. The data clearly define six communities, (although one community is only composed of one sample: Figure 2.5) within the three major bioregions suggested by Lombard *et al.* (2004). The 'outlier' or small patchy groups/communities are, according to Griffiths *et al*. (2010), the localized habitats, each within their own distinctive biota, that occur within the bioregions described by Lombard *et al.* (2004). It is possible, and highly likely, that more

intense sampling within the area will produce a more distinct geographical pattern that can be linked to environmental variables, as the current study exhibits a fairly course sampling resolution. On the other hand, these communities do not appear to have any geographical pattern, as indicated in Figure 2.9 below. It is possible that communities are randomly distributed, as according to McClain and Hardy (2010) found that many taxa are broadly distributed across the deep-sea floor, in spite of differing habitat type. For example they noted that seamount communities are made up of the same species found in the surrounding regions and therefore the seamounts are not islands of biodiversity, but rather consists of broadly distributed species. Only further sampling will tell.

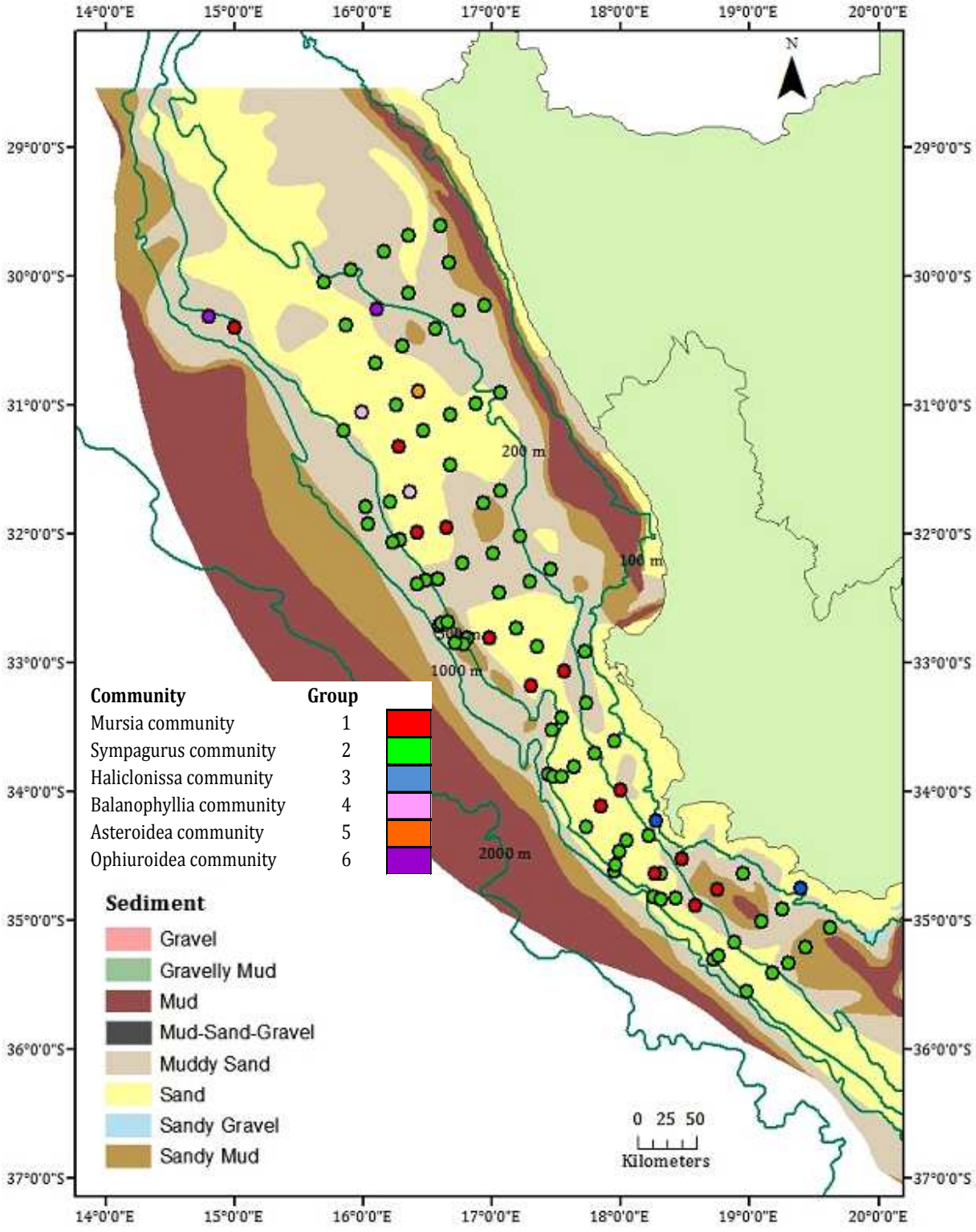


Figure 2.7. Sediment map (Dingle *et al.*, 1987) with Nansen West Coast groups/communities determined from hierarchical cluster analyses superimposed.

Chapter 3

BENTHIC INVERTEBRATE BIODIVERSITY AND DISTRIBUTION PATTERNS ALONG THE SOUTH AND WEST COASTS OF SOUTH AFRICA AS REVEALED BY AFRICANA TRAWL SURVEYS

3.1. Introduction

The distribution patterns and biogeographic zonation of South African intertidal and shallow marine benthic invertebrates are relatively well studied (Emanuel *et al*., 1992; Turpie *et al.*, 2000; Awad *et al.*, 2002; Lombard *et al.*, 2003; Griffiths *et al.*, 2010). Biogeographic distribution patterns for the inshore region have been analysed for mammals, fish, various invertebrate groups and algae (Emanuel *et al.*, 1992; Bolton *et al.*, 2004; Lombard *et al.*, 2004); however, a lack of literature existed on offshore diversity and biogeography, owing to the difficulties associated with deep-water sampling, such as the need for expensive equipment, time taken to lower gear to depth and large areas that need to be covered (Christie, 1974; Schalk, 1998; Ray and Grassle, 1991). Corliss *et al.,* (2009) noted that biodiversity in the deep sea is not well known, and that many environmental processes affecting diversity patterns are also not well understood, despite many studies addressing these questions. An understanding of oceanic biodiversity patterns has been particularly elusive, due to the difficulty in obtaining representative sample sets. While the inshore marine regions of South Africa are subject to the most intense anthropogenic impacts and activities, the offshore regions are not without concern (Shine, 2005). In view of the high existing and anticipated future levels of extraction of marine resources (fish and minerals; Lombard *et al.*, 2004), accurate information on the distribution of benthic invertebrate species is essential for management and conservation (Collaco *et al.*, 2003).

The current offshore bioregions recognized in South Africa are as follows: the Namaqua bioregion along the West Coast; the South western Cape bioregion stretching from offshore of Cape Point to offshore of Cape Columbine; the Agulhas Offshore bioregion; the Agulhas bioregion along the South Coast; the Natal bioregion from offshore of the Mbashe River in the Eastern Cape to Cape Vidal in KwaZulu-Natal; and the Delagoa bioregion further up along the Mozambique coast (Lombard *et al.*, 2004). The offshore bioregions are the West Indian Offshore bioregion, occurring offshore of the South and East Coasts and further offshore next to this region is the Indio-Pacific Bioregion at the edge of South Africa's Exclusive Economic Zone (EEZ: Lombard *et al.*, 2004). To date, however, these bioregions have been defined principally on the basis of water temperature and depth, rather than direct biological survey evidence. As a result, fewer offshore bioregions have been identified than coastal ones, as the water temperature becomes more homogenous offshore. This could be problematic, as each of these bioregions consists of a wide range of depth intervals, and depth has been shown to be a major factor delimiting benthic communities (Field, 1971; Christie, 1974; Hiller, 1994; Hernández-Arana *et al.*, 2003; Cleary *et al.*, 2005; Caranza *et al.*, 2008).

The EEZ of South Africa is extensive (1 075 272 km²), and under-sampled (see Chapter 1). Current knowledge of benthic invertebrate biodiversity and biogeography is based on some 1 460 dredge, 602 grab and 442 trawl samples (many more samples are reflected in museum collections, but the majority of these originate from directed collections of individual species or taxa, not on samples that examine the composition of the entire community). The patterns of community structure revealed by these samples have never been analysed in their entirety and there are problems with doing so; for example the collection dates of the samples span more than a century and a wide variety of different gear and collection methods have been used. Many reports have, however, analysed these data on a taxon-by-taxon basis (see Chapter 1). Some of the early samples originate from international expeditions of the late 1800's and early 1900's, such as the *Challenger, Valdivia* and *Gauss*, but the vast majority were collected during the 'University of Cape Town Ecological Survey', which took place from the 1950's to early 1980's. Within this period (1800's to 1980's) 2 504 benthic samples were collected. Virtually no benthic invertebrate surveys have been undertaken since that time. It should be noted that the majority of benthic samples were collected at depths of <100 m, with sample intensity declining rapidly with increasing depth. In the 0 - 100 m depth interval 39 samples were taken per 1 000 km², the most in any depth interval, but this is still a very small number on which to base community-level analyses. All other depth intervals (between 200 and 5 700 m) have less than five samples per 1000 km².

The findings of this study will provide benthic invertebrate baseline information for the West and South Coasts of South Africa. Such data are valuable for the selection and management of marine reserves, as well as highlighting areas in need of future research. The former Marine and Coast Management division of the South African government conducts annual fish surveys aboard the *F.R.S. Africana* along the West Coast (during January) and South Coast (during April) of South Africa. As all bycatch from trawling was discarded, this was seen as an opportunity to collect a representative series of macrofaunal samples that could be used in the determination of biogeographic patterns in the benthic environment. The trawling took place from depths of 50 to 700 m. It should be noted that only one type of habitat was surveyed, as only soft sediment could be trawled.

3.2. Study Area

The West Coast biomass survey covered the area from Cape Agulhas (34° 49'S, 20° 00'E) to the South African border with Namibia (29° 42'S, 17° 59'E), a nd from the coastline to the 700 m isobath (Figure 3.1). This cold-temperate region is characterized by the influence of the Benguela Current, which is the eastern boundary current of the South Atlantic subtropical gyre (Peterson and Stramma, 1991; Wedepohl *et al.*, 2000), beginning as a northward flow off the Cape of Good Hope, then moving up the western African coast towards the equator. The sources of the Benguela Current include: Indian and South Atlantic subtropical thermocline water; saline, low-oxygen tropical Atlantic water; and cooler, fresher sub-Antarctic water (Gyory *et al.*, 2002). The oceanography of the West Coast is dominated by wind-driven coastal upwelling, which

is perennial in the central latitudes (23° to 26°S) , and becomes more seasonal towards the northern (18°S) and southern (35°S) boundaries (Gibbons and Hutchings, 1996).

The South Coast biomass survey covered the area from 35 m to the 600 m isobath and from Cape Agulhas (34°49'S, 20°00'E) to East London (33°03'S, 27° 83'E; Figure 3.1). The Agulhas Current, which dominates this warm-temperate region, is the western boundary current of the South Indian Ocean and flows down the East Coast of Africa (Gordon, 1985). The source water for the Agulhas Current at its northern end is derived from the Mozambique Channel eddies (De Ruijter *et al.*, 2002) and the East Madagascar Current, but the greatest source of water is from recirculation from the southwest Indian Ocean sub-gyre (Gordon, 1985; Stramma and Lutjeharms, 1997). As the Agulhas Current reaches the southern tip of the continental shelf of Africa it retroflects and flows eastward as the Agulhas Return Current (Lutjeharms, 2006).

3.2.1. *F.R.S. Africana*

The F*.R.S. Africana* vessel was used to collect invertebrate data, in collaboration with the then Marine and Coastal Management Branch, Department of Environmental Affairs and Tourism, who carry out demersal trawl surveys annually off the West Coast and South Coast of South Africa. Trawl locations were selected in a pseudo-random sampling method, due to the fact that only unconsolidated bottom sediment can be trawled. Sampling depth ranged between 30 - 700 m along the continental shelf and upper slope. Using a 5x5 minute grid cell, the number of stations per depth and longitude stratum was directly proportional to the area of each stratum. A 35 m German trawl net, with multi-purpose Morgere "Butterfly" doors, was deployed, the cod-end being lined with pilchard netting in the form of a sleeve in order to retain all small fish and larger invertebrates. Door-spread, vertical mouth opening and width spread were monitored with acoustic sensors from Simrad.

3.3. Materials and Methods

During this study invertebrates were collected as bycatch on two surveys that took place along the South Coast and West Coast of South Africa. Each survey lasted six weeks from which a total of 95 (South Coast) and 105 (West Coast) trawl samples were collected. Each trawl was dragged along the seafloor for 30 min. Once on deck invertebrates were sorted to species level where possible, then photographed and weighed wet. Representative specimens of any species that could not be identified in the field were preserved in 70% ethanol or 10% formalin, and returned to the University of Cape Town for further taxonomic study.

3.3.1. Sampling sites

The Africana South Coast survey sampling sites were located between 34°49'S, 20°00'E and 33°03'S, 27°8'E, while the Africana West Coast survey sampling sites were located between 34°49'S, 20°00'E and 29°42'S, 17°59'E (Figure 3.1). Samples were collected whilst travelling generally along a North-Easterly

route for the first 75 sites, followed by a Westerly route for the next 20 sites. On the West Coast survey, the Africana generally followed a North to North-Easterly route, whilst collecting samples from 105 sites. In total 1 774.12 ha were sampled during the two surveys, 801.99 ha offshore of the South Coast and 972.13 ha offshore of the West Coast.

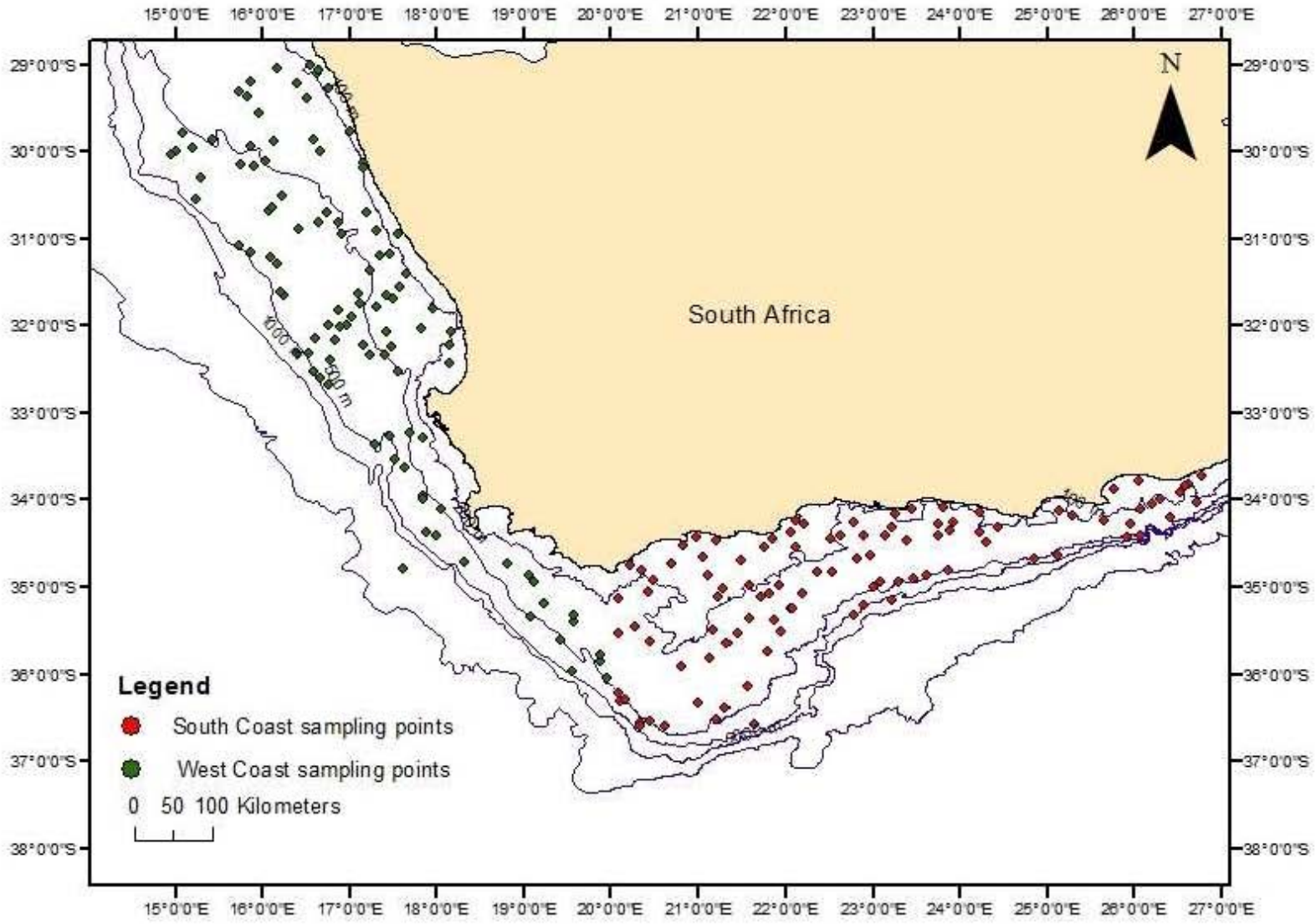


Figure 3.1. The sampling points surveyed along the West Coast and South Coast of South Africa.

3.3.2. Statistical methods

For materials and methods used, and in order to avoid repetition please refer back to Chapter 2, sections 2.3.2, 2.3.3 and 2.4.1.

3.3.3. Multiple linear regression analysis

The aim was to construct multiple linear regression models to predict the levels of species diversity using environmental variables as predictors. For this purpose, the data from the Africana South Coast and West Coast surveys were pooled. The dependent variable was species richness, measured as a continuous quantitative variable. The generalized regression equation for each model was:

$$\hat{Y} = \beta_0 + \beta_1 X_1 + ... \beta_k X_k + \varepsilon$$

where: $\hat{Y}$ is the predicted value of the dependent variable Y (the species diversity index); β_0 is the intercept (the value of $\hat{Y}$ when all values of X are zero); $\beta_1 ..... \beta_k$ are the estimated partial regression (β) coefficients for k predictor (X) variables; and ε = the residual error (the difference between the fitted and the observed value of Y).

Four continuous predictor variables measured at the interval/ratio level were depth (m), dissolved oxygen (DO (mg/L), salinity, and temperature ($^{\circ}$C). One nominal categorical variable was included to define the survey area, expressed as a dummy variable (1 = South Coast and 0 = West Coast). Three nominal categories of substrate composition were also included, specifically sand, sand and mud, and mud. The substrate composition was expressed as three dummy variables (1 = sand; 0 = other substrates; 1 = sand and mud; 0 = other substrates; 1 = mud; 0 = other substrates).

Regression is a parametric technique that assumes normally distributed variables, but remains robust if the distributions are slightly skewed (Tabachnik and Fidell, 2007). Species richness and the environmental variables were observed to deviate very strongly from normality. Logarithmic ($\log_{10}$) transformation of species richness, depth, salinity, temperature, and a squared transformation of DO were used to approximately normalize the variables. Transformations also helped to avoid violations of the assumptions of linear regression (Tabachnik and Fidell, 2007). These assumptions were (a) linear relationships between the dependent and predictor variables; (b) residual normality; (c) homogeneity of variance of the dependent variable across all the predictor variables; (d) minimal collinearity (i.e. inter-correlation of the predictor variables; and (e) minimal autocorrelation or independence of the residual errors in the successive values of the dependent variable collected in a time series.

Linearity was checked using correlation analysis. The decision rule was to reject the null hypothesis of no significant correlation if $p < 0.05$ for the correlation coefficient. When inter-correlation is excessive, the standard errors are inflated, influencing the magnitudes and signs of the regression coefficients, making

statistical inferences difficult. There is no objective test to determine whether or not multi-collinearity is a problem. It is up to the researcher to decide, depending upon how rigorous he/she wants to be (0'Brien, 2003). The Variance Inflation Factor (VIF) is the most commonly used measure of the impact of collinearity. The VIF is always ≥ 1. In this study, VIF > 5 was used to indicate collinearity, but this is just one of many arbitrary cut-off criteria for deciding when there is too much collinearity (O'Brien, 2003). Some researchers get concerned when the VIF is over 2.5 (Alison, 1998).

Autocorrelation was checked using the Durbin Watson (D-W) statistic. Small values of D-W (<2) indicated auto-correlation. The critical values of D-W for k predictor variables and N sampling sites were found in a statistical table. If the computed D-W statistic was less than the critical value then autocorrelation was significant at $p < 0.05$. A model describing the autocorrelation between samples can be written (Diggle and Ribeiro, 2007), however it is not within the scope of this project to do so.

The standard error (SE) and t statistic were computed for each regression coefficient (β). The decision rule was to reject the null hypothesis that β was zero if $p < 0.05$ for the t statistic, where $t = \beta/SE$. If collinearity was found to inflate the standard errors and biased the results of the t tests, then the collinear variables were combined.

The R^2 value, adjusted for the number of predictor variables, was recorded to provide a measure of the effect size, i.e. the proportion of the variance in the species diversity indices that could be explained by the variance in the predictor variables.

3.4. Results

3.4.1. Substratum

The South Coast of South Africa is made primarily made up of Sand (Lombard et al., 2004). Over two thirds of the substratum samples collected on the Africana South Coast survey contained only sand, while approximately 1% consisted only of mud (Figure 3.2). The other samples included mixtures of sand and mud in various proportions, occasionally with gravel. The sediment on the West Coast of South Africa consists maily of Sand and muddy-sand (Lombard et al., 2004). On the Africana West Coast survey, one third of the substratum samples contained only sand, whereas just under one quarter consisted of muddy-sand, and the remainder were variable mixtures of sand and mud, rarely with gravel (Figure 3.2).

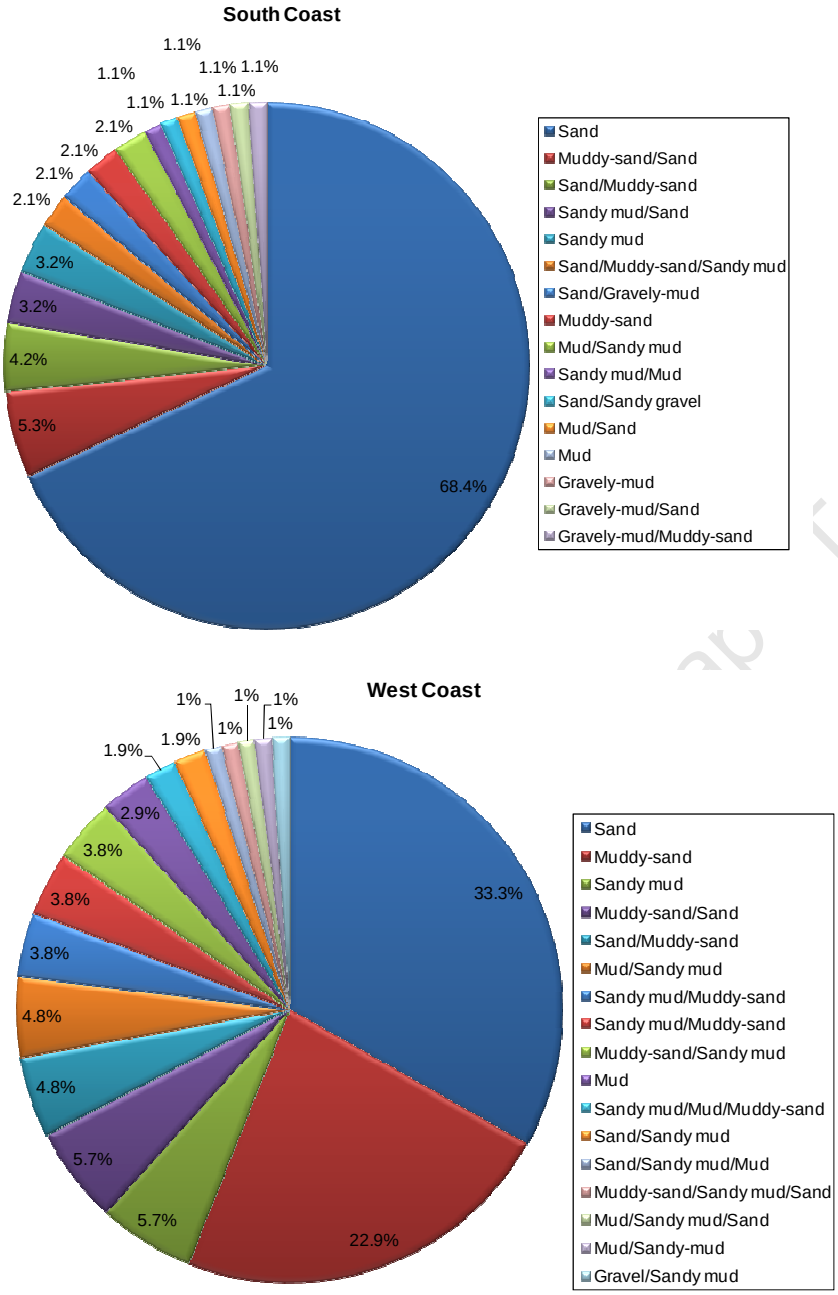


Figure 3.2. The substratum composition according to Lombard *et al.,* (2004) in the region where the South Coast and West Coast surveys took place.

3.4.2. Depth, dissolved oxygen (DO), salinity and temperature

The physico-chemical environmental variables collected on the two surveys are summarized in Table 3.1.

The sampling sites on the South Coast were on average shallower (mean depth = 136.2 m, ± 92, S.E. = 9) and covered a slightly wider range of depths than those on the West Coast (mean depth = 235.1 m, ± 116, S.E. = 0.01). The DO levels were generally lower in the bottom water for the South Coast (mean = 2.15 mg/L, ± 0.45, S.E. = 0.05) than in the bottom water for the West Coast (mean = 2.94 mg/L, ± 0.81, S.E. = 0.09). The salinity of the bottom water at the sampling sites on the South Coast covered a wider and elevated range (34.54 - 35.09, ±0.1, S.E. = 0.01) than those on the West Coast (34.32 - 34.82, ±0.12, S.E. = 0.01). The bottom water temperatures were also generally higher for the South Coast (mean = 10.1^{o}C, ± 1.1, S.E. = 0.1) compared to the West Coast (mean = 8.4^{o}C, ± 1.3, S.E. = 0.1).

Table 3.1. Summary of the environmental data for depth, dissolved oxygen (DO), salinity and temperature, collected along the South and West Coasts of South Africa.

		Depth (m)	DO (mg/L)	Salinity	Temperature (oC)
F.R.S. Africana South Coast	Number of samples	95	87	87	87
	Mean	136	2.94	34.83	10.1
	Median	112	3.05	34.84	10.2
	Minimum	35	1.52	34.54	6.2
	Maximum	572	3.76	35.09	13.2
	Range	537	2.24	0.55	7.0
	Variance	8460	0.20	0.01	1.2
	Standard deviation	92	0.45	0.10	1.1
	Standard error (S.E)	9	0.05	0.01	0.1
F.R.S. Africana West Coast	Number of samples	105	88	88	88
	Mean	235	2.15	34.62	8.4
	Median	203	2.22	34.63	8.7
	Minimum	58	0.29	34.32	4.6
	Maximum	608	3.52	34.82	10.5
	Range	550	3.23	0.50	5.9
	Variance	1348	0.66	0.02	1.8
	Standard deviation	116	0.81	0.12	1.3
	Standard error	11	0.09	0.01	0.1

3.4.3. Depth

The topography of the seafloor on the South and West Coasts were very different. The 3D wireframe maps (Figure 3.3) illustrate that the seafloor of the South Coast survey area was relatively flat, permeated by several deep trenches, whereas the continental shelf ran diagonally across the West Coast survey area.

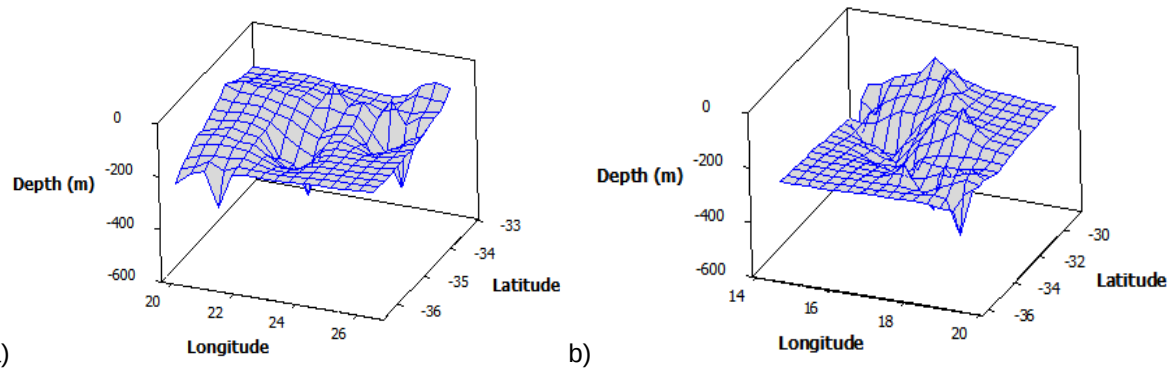


Figure 3.3. Three dimensional topography map of the seafloor for the a) South Coast and b) West Coast survey areas. Based on the coordinates and depths from which samples were collected aboard the *F.R.S. Africana*.

3.4.4. Faunal composition

The abundance and biomass was averaged per hectare (ha). The abundance of the benthic epifauna (Table 3.2) was generally lower among the samples from the South Coast (mean = 16 individuals/ha, ± 1.24, S.E. = 0.13) than those from the West Coast (mean = 54 individuals/ha, ± 0.66, S.E. = 0.06). Similarly the biomass of epifauna was generally lower among the samples from the South Coast (mean = 175.48 g/ha, ± 237.07, S.E. = 24.32) than those from the West Coast (mean = 186.45 g/ha, ± 180.93, S.E. = 17.66).

Table 3.2. Biomass and abundance statistics of the benthic epifauna collected during the Africana South and West Coast surveys.

		Relative abundance (individuals/ha)	Biomass
South Coast	Number of samples	95	95
	Mean	16	175.48
	Median	5	96.51
	Minimum	0	6.79
	Maximum	406	1054.3
	Variance	1.54	56204.19
	Standard deviation	1.24	237.07
	Standard error	0.13	24.32
West Coast	Number of samples	105	105
	Mean	54	186.45
	Median	17	125.78
	Minimum	0	3.36
	Maximum	973	1220.01
	Variance	0.44	32734.94
	Standard deviation	0.66	180.93
	Standard error	0.06	17.66

A total of 135 species in nine phyla were identified, 95 from the South Coast and 67 from the West Coast (Table 3.3). The pie chart (Figure 3.4) reveals that the samples from the South Coast were numerically dominated by *Brisaster capensis* sp., Echinoidea (28.8%); *Sympagurus dimorphus*, Malacostraca (22.4%) and *Pleurobranchea bubala*, Gastropoda (10.2%). The samples from the West Coast were numerically dominated by *Suberites* sp., Demospongiae (44.2%); *Sympagurus dimorphus*, Malacostraca (28.9%); and *Pterygosquilla armata*, Malacostraca (12.6%).

Table 3.3. The number of species of benthic epifauna collected during the combined two Africana surveys, identified to class level.

Phylum	Class	South Coast	West Coast
Annelida	Polychaeta	2	2
Arthropoda	Malacostraca	26	19
Arthropoda	Pycnogonida	2	0
Bryozoa	Gymnolaemata	2	2
Chordata	Ascidiacea	4	0
Cnidaria	Anthozoa	5	2
Cnidaria	Hydrozoa	5	1
Cnidaria	Cnidaria	0	4
Echinodermata	Asteroidea	16	13
Echinodermata	Crinoidea	0	3
Echinodermata	Echinoidea	5	4
Echinodermata	Ophiuroidea	4	1
Echinodermata	Holothuroidea	1	0
Mollusca	Gastropoda	17	13
Porifera	Hexactinellida	1	1
Porifera	Demospongiae	0	2
Porifera	Unknown Porifera	5	0
		95	67

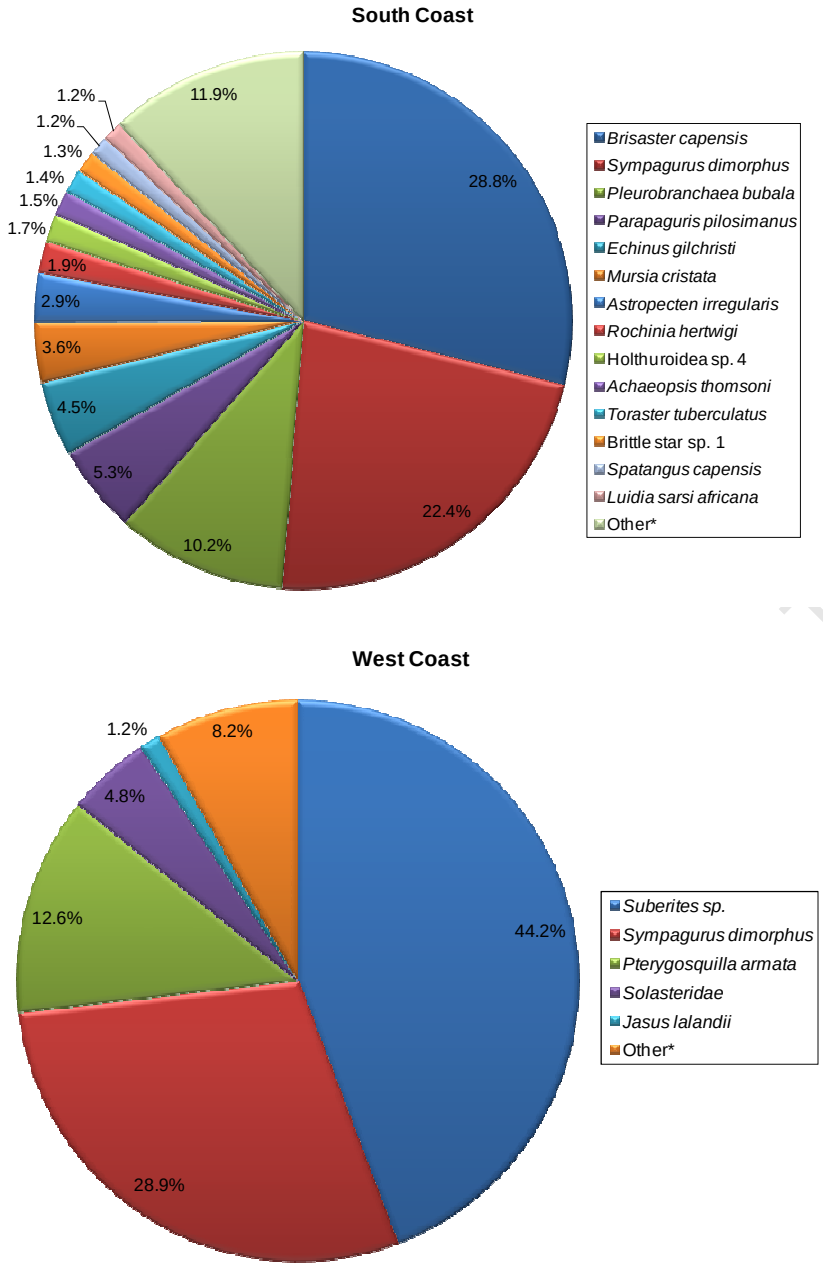


Figure 3.4. Species composition of epibenthic fauna in terms of abundance levels collected in the two survey areas, South and West Coasts (* species grouped as 'other' each represented <1% of the total biomass).

The composition of the fauna recorded from both the South and West Coast surveys, based on abundance, is given in Table 3.4. A higher total of 51 503 individuals were sampled from the South Coast compared to 13 326 from the West Coast. Only 26.4% of species collected were common to both the South Coast and West Coast surveys.

Table 3.4. The species composition of the benthic epifaunal abundance collected offshore of the South and West Coasts of South Africa, in total abundance, abundance per hectare and percentage frequency.

Phylum	Species	South Coast			West Coast		
		Individuals	Individuals per ha	Percent (%)	Individuals	Individuals per ha	Percent (%)
Annelida	Euphrosine sp.	42	4.98	0.32	8	0.86	0.02
	Polychaeta sp. 2	7	0.83	0.05	0	0	0
	Polychaeta sp. 6	0	0	0	237	25.6	0.46
Arthropoda	Achaeopsis spinulosus	55	6.52	0.41	0	0	0
	Achaeopsis thomsoni	195	23.1	1.46	44	4.75	0.09
	Agononida incerta	0	0	0	3	0.32	0.01
	Anomura sp. 1	2	0.24	0.02	0	0	0
	Anomura sp. 7	2	0.24	0.02	0	0	0
	Brachyura sp. 1	8	0.95	0.06	0	0	0
	Dardanus arrosor	11	1.3	0.08	0	0	0
	Dromidia hirsutissima	2	0.24	0.02	0	0	0
	Exodromidia spinosa	0	0	0	201	21.71	0.39
	Geryon sp.	0	0	0	50	5.40	0.10
	Goneplax rhomboides	73	8.65	0.55	0	0	0
	Homola barbata	32	3.79	0.24	0	0	0
	Macropodia formosa	27	3.2	0.20	0	0	0
	Merhippolyte calmani	0	0	0	18	1.94	0.04
	Mursia cristiata	484	57.33	3.63	55	5.94	0.11
	Ovalipes iridescens	13	1.54	0.10	0	0	0
	Ovalipes punctatus	31	3.67	0.23	0	0	0
	Palinurus gilchristi	33	3.91	0.25	8	0.86	0.02
	Pallenopsis capensis	59	6.99	0.44	0	0	0
	Paracilicaea clavus	2	0.24	0.02	0	0	0
	Parapallene algoae	10	1.18	0.08	0	0	0
	Plesionika martia	0	0	0	29	3.13	0.06

Phylum	Species	South Coast			West Coast		
		Individuals	Individuals per ha	Percent (%)	Individuals	Individuals per ha	Percent (%)
	Pentacheles validus	0	0	0	32	3.46	0.06
	Pseudodromia rotunda	74	8.77	0.56	0	0	0
	Pseudodromia rotunda sp.	2	0.24	0.02	0	0	0
	Pterygosquilla armata	23	2.72	0.17	6498	701.88	12.62
	Rochinia hertwigi	256	30.32	1.92	41	4.43	0.08
	Rocinela granulosa	19	2.25	0.14	0	0	0
	Scyllarides elisabethae	6	0.71	0.05	0	0	0
	Solenocera algoensis	0	0	0	45	4.86	0.09
	Swimming brachyura sp. 1	0	0	0	118	12.75	0.23
	Cardisoma carnifex	3	0.36	0.02	0	0	0
	Chaceon quinquedens	0	0	0	27	2.92	0.05
	Funchalia woodwardi	6	0.71	0.05	33	3.56	0.06
	Jasus lalandii	0	0	0	642	69.35	1.25
	McPherasoni crab	0	0	0	6	0.65	0.01
	Parapaguris pilosimanus	711	84.22	5.34	316	34.13	0.61
	Diogenes brevirostris	10	1.18	0.08	0	0	0
	Sympagurus dimorphus	2991	354.3	22.45	14878	1607	28.9
Bryozoa	Bryozoa sp. 1	0	0	0	2	0.22	0
	Bryozoa sp. 2	4	0.47	0.03	6	0.65	0.01
	Bryozoa sp. 3	3	0.36	0.02	0	0	0
Chordata	Ascidiacea sp. 1	36	4.26	0.27	0	0	0
	Ascidiacea sp. 2	5	0.59	0.04	0	0	0
	Ascidiacea sp. 4	3	0.36	0.02	0	0	0
	Ascidicea sp. 10	4	0.47	0.03	0	0	0
Cnidaria	Actinoptilum molle	81	9.59	0.61	86	9.29	0.17
	Coral sp. 11	8	0.95	0.06	0	0	0
	Coral sp. 7	7	0.83	0.05	0	0	0
	Hydrozoa sp. 1	10	1.18	0.08	0	0	0

Phylum	Species	South Coast			West Coast		
		Individuals	Individuals per ha	Percent (%)	Individuals	Individuals per ha	Percent (%)
	Hydrozoa sp. 12	2	0.24	0.02	0	0	0
	Hydrozoa sp. 2	11	1.3	0.08	0	0	0
	Hydrozoa sp. 20	0	0	0	2	0.22	0
	Hydrozoa sp. 3	5	0.59	0.04	0	0	0
	Hydrozoa sp. 8	3	0.36	0.02	0	0	0
	Sea pen sp. 2	0	0	0	4	0.43	0.01
	Cnidaria sp. 1	42	4.98	0.32	85	9.18	0.17
	Cnidaria sp. 2	0	0	0	187	20.2	0.36
	Cnidaria sp. 3	35	4.15	0.26	49	5.29	0.10
	Cnidaria sp. 4	0	0	0	425	45.91	0.83
Echinoder-mata	Asteroidea sp. 12	8	0.95	0.06	0	0	0
	Asteroidea sp. 18	3	0.36	0.02	0	0	0
	Asteroidea sp. 22	2	0.24	0.02	0	0	0
	Asteroidea sp. 26	3	0.36	0.02	0	0	0
	Asteroidea sp. 35	0	0	0	36	3.89	0.07
	Asteroidea sp. 36	0	0	0	424	45.8	0.82
	Asteroidea sp. 6	7	0.83	0.05	0	0	0
	Asteroidea sp. 7	34	4.03	0.26	7	0.76	0.01
	Astropecten irregularis	388	45.96	2.91	317	34.24	0.62
	Blue astropecten	0	0	0	85	9.18	0.17
	Brisaster capensis	9	1.07	0.07	0	0	0
	Brisaster capensis sp.	3842	455.11	28.83	67	7.24	0.13
	Brittle star sp. 1	173	20.49	1.30	18	1.94	0.04
	Calliaster acanthodes	7	0.83	0.05	0	0	0
	Crinoidea sp. 10	0	0	0	267	28.84	0.52
	Crinoidea sp. 11	0	0	0	3	0.32	0.01
	Crinoidea sp. 200	0	0	0	20	2.16	0.04

Phylum	Species	South Coast			West Coast		
		Individuals	Individuals per ha	Percent (%)	Individuals	Individuals per ha	Percent (%)
	Echinus gilchristi	605	71.67	4.54	18	1.94	0.04
	Gorgonocephalus eucnemis	70	8.29	0.53	0	0	0
	Holothuroidea sp. 4	222	26.3	1.67	0	0	0
	Luidia sarsi africana	162	19.19	1.22	28	3.02	0.05
	Marthasterias glacialis	63	7.46	0.47	0	0	0
	Odontaster australis	0	0	0	24	2.59	0.05
	Ophiuroidea sp. 2	8	0.95	0.06	0	0	0
	Ophiuroidea sp. 5	10	1.18	0.08	0	0	0
	Persephonaster agassizi	49	5.8	0.37	117	12.64	0.23
	Pteraster capensis	18	2.13	0.14	0	0	0
	Pteraster capensis sp.	0	0	0	9	0.97	0.02
	Solasteridae	77	9.12	0.58	2481	267.98	4.82
	Spatangus capensis	164	19.43	1.23	221	23.87	0.43
	Stereocidaris excavat	22	2.61	0.17	0	0	0
	Toraster tuberculatus	185	21.91	1.39	99	10.69	0.19
	Urchin sp. 1	0	0	0	5	0.54	0.01
	Henricia abyssalis	0	0	0	7	0.76	0.01
	Pseudarchaster tesselatus	8	0.95	0.06	169	18.25	0.33
	Pseudocnella insolens	73	8.65	0.55	0	0	0
Mollusca	Amalda bullioides	0	0	0	3	0.32	0.01
	Dermatobranchus sp. 4	14	1.66	0.11	0	0	0
	Fasciolaria lugubris lugubris	3	0.36	0.02	0	0	0
	Fasciolaria sp.	0	0	0	48	5.18	0.09
	Fusitriton magellanicus	2	0.24	0.02	0	0	0
	Hastula rufopunctata	14	1.66	0.11	2	0.22	0
	Kaloplocamus ramosus	12	1.42	0.09	0	0	0
	Mollusca sp. 1	5	0.59	0.04	0	0	0
	Mollusca sp. 3	3	0.36	0.02	0	0	0

Phylum	Species	South Coast			West Coast		
		Individuals	Individuals per ha	Percent (%)	Individuals	Individuals per ha	Percent (%)
	Mollusca sp. 51	0	0	0	7	0.76	0.01
	Opisthobranch sp. 40	0	0	0	16	1.73	0.03
	Opisthobranch sp. 41	0	0	0	2	0.22	0
	Opisthobranchia sp. 1	19	2.25	0.14	0	0	0
	Opisthobranchia sp. 2	21	2.49	0.16	0	0	0
	Opisthobranchia sp. 3	72	8.53	0.54	0	0	0
	Opisthobranchia sp. 4	36	4.26	0.27	0	0	0
	Peristernia forskalii	27	3.2	0.20	0	0	0
	Triviella calvariola	6	0.71	0.05	0	0	0
	Athleta abyssicola	2	0.24	0.02	0	0	0
	Athleta disparilis	0	0	0	2	0.22	0
	Athleta lutosa	0	0	0	4	0.43	0.01
	Athleta sp. 1	0	0	0	7	0.76	0.01
	Athleta sp. 2	0	0	0	8	0.86	0.02
	Fusinus ocellifer	19	2.25	0.14	0	0	0
	Neptuneopsis gilchristi	0	0	0	7	0.76	0.01
	Philine aperta	20	2.37	0.15	12	1.3	0.02
	Pleurobranchaea bubala	1361	161.22	10.21	0	0	0
	White Opisthobranch sp.	0	0	0	20	2.16	0.04
Porifera	Porifera sp. 1	4	0.47	0.03	0	0	0
	Porifera sp. 13	2	0.24	0.02	0	0	0
	Porifera sp. 15	4	0.47	0.03	0	0	0
	Porifera sp. 2	8	0.95	0.06	0	0	0
	Porifera sp. 4	4	0.47	0.03	0	0	0
	Rosella antarctica	0	0	0	10	1.08	0.02
	Suberites sp.	0	0	0	22785	2461	44.26
	Mycale massa	8	0.95	0.06	13	1.4	0.03
TOTAL		13326	1578	100	51503	55630	100

Figure 3.5 shows the composition of the fauna in terms of biomass. On the South Coast the most important species in terms of biomass were *Sympagurus dimorphus*, Malacostraca (13.6%); *Pleurobranchaea bubala*, Gastropoda (10.5%); *Spatangus capensis*, Echinoidea (8.6%); *Brisaster capensis* sp., Echinoidea (7.9%) and *Echinus gilchristi*, Echinoidea (6.1%). The biomass collected from the West Coast was dominated by *Jasus lalandii*, Malacostraca (16.9%); *Sympagurus dimorphus*, Malacostraca (12.3%); *Pterygosquilla armata*, Malacostraca (11.2%); *Suberites* sp., Demospongiae (9.1%) and *Spatangus capensis*, Echinoidea (6.4%). The percentage compositions of all species by biomass are listed in Table 3.5. The total biomass collected from the South Coast was 143 821.6 g (179.3 g/ha) compared to 210 987.5 g (217.04 g/ha) from the West Coast.

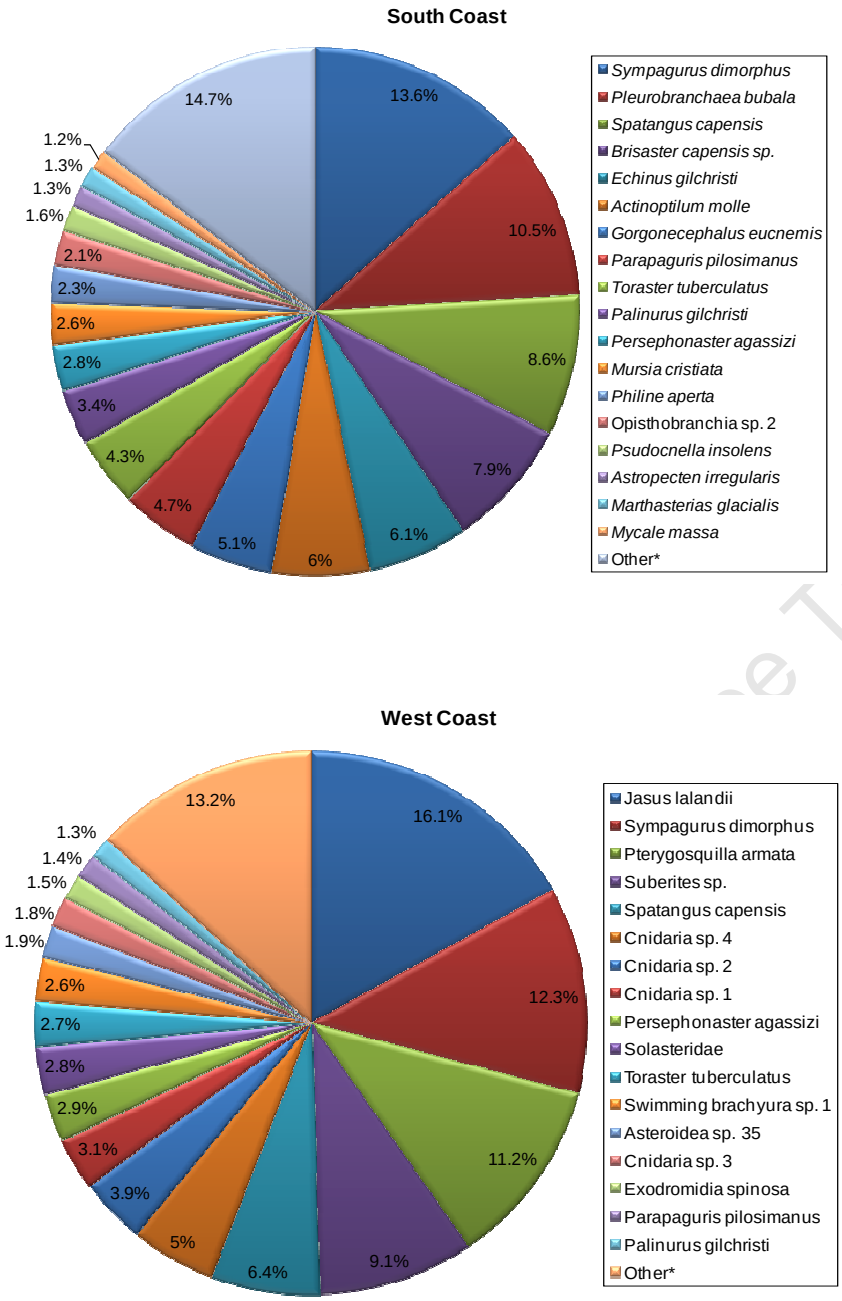


Figure 3.5. Species composition of epibenthic faunal biomass collected offshore of the South Coast and West Coast of South Africa (* each of the other species represented <1% of the total biomass).

Table 3.5. Species composition of the benthic epifaunal biomass collected along the South and West Coasts of South Africa, according to the total biomass, biomass per hectare and percentage.

Phylum	Species	South Coast Total biomass (g)	Mean biomass per hectare (g/ha)	Percent (%)	West Coast Total biomass (g)	Mean biomass per hectare (g/ha)	Percent (%)
Annelida	Euphrosine sp.	179.1	21.22	0.124	56.3	6.08	0.027
	Polychaeta sp. 2	43.8	5.19	0.030	0	0	0
	Polychaeta sp. 6	0	0	0	488.2	52.73	0.231
Arthropoda	Achaeopsis spinulosus	205.5	24.34	0.143	0	0	0
	Achaeopsis thomsoni	428	50.7	0.298	69.7	7.53	0.033
	Agononida incerta	0	0	0	16.7	1.8	0.008
	Anomura sp. 1	38.4	4.55	0.027	0	0	0
	Anomura sp. 7	14.8	1.75	0.010	0	0	0
	Brachyura sp. 1	16.3	1.93	0.011	0	0	0
	Dardanus arrosor	1070.9	126.85	0.745	0	0	0
	Dromidia hirsutissima	62.2	7.37	0.043	0	0	0
	Exodromidia spinosa	0	0	0	3091.6	333.94	1.465
	Geryon sp.	0	0	0	2122.5	229.26	1.006
	Goneplax rhomboides	461.8	54.7	0.321	0	0	0
	Homola barbata	151.5	17.95	0.105	0	0	0
	Macropodia formosa	427	50.58	0.297	0	0	0
	Merhippolyte calmani	0	0	0	36.9	3.99	0.017
	Mursia cristiata	3697.8	438.02	2.571	695.3	75.1	0.330
	Ovalipes iridescens	1033.8	122.46	0.719	0	0	0
	Ovalipes punctatus	487.4	57.74	0.339	0	0	0
	Palinurus gilchristi	4865.1	576.3	3.383	2672	288.62	1.266
	Pallenopsis capensis	73.6	8.72	0.051	0	0	0
	Paracilicaea clavus	4.3	0.51	0.003	0	0	0
	Parapallene algoae	8.4	1	0.006	0	0	0
	Plesionika martia	0	0	0	383.7	41.45	0.182

Phylum	Species	South Coast					
		Total biomass (g)	Mean biomass per hectare (g/ha)	Percent (%)	Total biomass (g)	Mean biomass per hectare (g/ha)	Percent (%)
	Pentacheles validus	0	0	0	203.4	21.97	0.092
	Pseudodromia rotunda	697.2	82.59	0.485	0	0	0
	Pseudodromia rotunda sp.	10.5	1.24	0.007	0	0	0
	Pterygosquilla armata	84.6	10.02	0.059	23558.9	2544.71	11.166
	Rochinia hertwigi	1375.7	162.96	0.957	71.1	7.68	0.034
	Rocinela granulosa	73.4	8.69	0.051	0	0	0
	Scyllarides elisabethae	1613.8	191.16	1.122	0	0	0
	Solenocera algoensis	0	0	0	360.7	38.96	0.171
	Swimming Brachyura sp. 1	0	0	0	5501.9	594.29	2.608
	Cardisoma carnifex	266.4	31.56	0.185	0	0	0
	Chaceon quinquedens	0	0	0	375	40.51	0.178
	Funchalia woodwardi	103.1	12.21	0.072	302.6	32.69	0.143
	Jasus lalandii	0	0	0	35752.8	3861.83	16.945
	McPherasoni crab	0	0	0	1762	190.32	0.835
	Diogenes brevirostris	44.3	5.25	0.031	0	0	0
	Parapaguris pilosimanus	6784.8	803.7	4.718	2977.9	321.66	1.411
	Sympagurus dimorphus	19515.8	2311.75	13.569	26025.3	2811.11	12.335
Bryozoa	Bryozoa sp. 1	0	0	0	10.2	1.1	0.005
	Bryozoa sp. 2	61.1	7.24	0.042	11.3	1.22	0.005
	Bryozoa sp. 3	25.1	2.97	0.017	0	0	0
Chordata	Ascidiacea sp. 1	201	23.81	0.140	0	0	0
	Ascidiacea sp. 2	194.9	23.09	0.136	0	0	0
	Ascidiacea sp. 4	192.4	22.79	0.134	0	0	0
	Ascidiacea sp. 10	15	1.78	0.010	0	0	0
Cnidaria	Actinoptilum molle	8611.8	1020.11	5.988	2269.8	245.17	1.076
	Coral sp. 11	11.9	1.41	0.008	0	0	0
	Coral sp. 7	99.6	11.80	0.069	0	0	0

Phylum	Species	South Coast			West Coast		
		Total biomass (g)	Mean biomass per hectare (g/ha)	Percent (%)	Total biomass (g)	Mean biomass per hectare (g/ha)	Percent (%)
	Hydrozoa sp. 1	249.8	29.59	0.174	0	0	0
	Hydrozoa sp. 12	32.4	3.84	0.023	0	0	0
	Hydrozoa sp. 2	187.8	22.25	0.131	0	0	0
	Hydrozoa sp. 20	0	0	0	10	1.08	0.005
	Hydrozoa sp. 3	10.7	1.27	0.007	0	0	0
	Hydrozoa sp. 8	6.7	0.79	0.005	0	0	0
	Sea pen sp. 2	0	0	0	515.4	55.67	0.244
	Cnidaria sp. 1	646.6	76.59	0.450	6643.3	717.57	3.149
	Cnidaria sp. 2	0	0	0	8137.2	878.94	3.857
	Cnidaria sp. 3	224	26.53	0.156	3741.8	404.17	1.773
	Cnidaria sp. 4	0	0	0	10457.9	1129.61	4.957
Echino-dermata	Asteroidea sp. 12	48.6	5.76	0.034	0	0	0
	Asteroidea sp. 18	4.2	0.5	0.003	0	0	0
	Asteroidea sp. 22	10.1	1.2	0.007	0	0	0
	Asteroidea sp. 26	110.1	13.04	0.077	0	0	0
	Asteroidea sp. 35	0	0	0	4043.9	436.80	1.917
	Asteroidea sp. 36	0	0	0	1580.7	170.74	0.749
	Asteroidea sp. 6	11.2	1.33	0.008	0	0	0
	Asteroidea sp. 7	580	68.7	0.403	105.1	11.35	0.050
	Astropecten irregularis	1903.9	225.53	1.324	1837.9	198.52	0.871
	Blue astropecten	0	0	0	467.3	50.48	0.221
	Brisaster capensis	396.4	46.96	0.276	0	0	0
	Brisaster capensis sp.	11321.5	1341.09	7.872	776.1	83.83	0.368
	Brittle star sp. 1	247.4	29.31	0.172	14.4	1.56	0.007
	Calliaster acanthodes	285.1	33.77	0.198	0	0	0
	Crinoidea sp. 10	0	0	0	117.3	12.67	0.056
	Crinoidea sp. 11	0	0	0	8.4	0.91	0.004
	Crinoidea sp. 200	0	0	0	3.4	0.37	0.002

Phylum	Species	South Coast			West Coast		
		Total biomass (g)	Mean biomass per hectare (g/ha)	Percent (%)	Total biomass (g)	Mean biomass per hectare (g/ha)	Percent (%)
	Echinus gilchristi	8775.7	1039.53	6.102	1559.2	168.42	0.739
	Gorgonocephalus eucnemis	7277.9	862.11	5.060	0	0	0
	Holothuroidea sp. 4	380.2	45.04	0.264	0	0	0
	Luidia sarsi africana	1538.5	182.24	1.070	478.7	51.71	0.227
	Marthasterias glacialis	1883.1	223.06	1.309	0	0	0
	Odontaster australis	0	0	0	313.7	33.88	0.149
	Ophiuroidea sp. 2	132.4	15.68	0.092	0	0	0
	Ophiuroidea sp. 5	11	1.3	0.008	0	0	0
	Persephonaster agassizi	4059.6	480.88	2.823	6208.1	670.57	2.942
	Pteraster capensis	520.2	61.62	0.362	0	0	0
	Pteraster capensis sp.	0	0	0	1159	125.19	0.549
	Solasteridae	855.6	101.35	0.595	5881.3	635.27	2.788
	Spatangus capensis	12334.7	1461.11	8.576	13484.3	1456.5	6.391
	Stereocidaris excavat	539	63.85	0.375	0	0	0
	Toraster tuberculatus	6222.4	737.08	4.326	5659.5	611.31	2.682
	Urchin sp. 1	0	0	0	183.4	19.81	0.087
	Henricia abyssalis	0	0	0	20.7	2.24	0.010
	Pseudarchaster tesselatus	267.2	31.65	0.186	2141.7	231.34	1.015
	Pseudocnella insolens	2261.9	267.93	1.573	0	0	0
Mollusca	Amalda bullioides	0	0	0	16	1.73	0.008
	Dermatobranchus sp. 4	16.8	1.99	0.012	0	0	0
	Fasciolaria lugubris lugubris	89.2	10.57	0.062	0	0	0
	Fasciolaria sp.	0	0	0	1944.6	210.05	0.922
	Fusitriton magellanicus	102	12.08	0.071	0	0	0
	Hastula rufopunctata	64.8	7.68	0.045	6.2	0.67	0.003
	Kaloplocamus ramosus	45.4	5.38	0.032	0	0	0
	Mollusca sp. 1	108.2	12.82	0.075	0	0	0

Phylum	Species	South Coast Total biomass (g)	Mean biomass per hectare (g/ha)	Percent (%)	West Coast Total biomass (g)	Mean biomass per hectare (g/ha)	Percent (%)
	Mollusca sp. 3	6.6	0.78	0.005	0	0	0
	Mollusca sp. 51	0	0	0	58.8	6.35	0.028
	Opisthobranch sp. 40	0	0	0	176.9	19.11	0.084
	Opisthobranch sp. 41	0	0	0	9.2	0.99	0.004
	Opisthobranchia sp. 1	573.4	67.92	0.399	0	0	0
	Opisthobranchia sp. 2	3027.2	358.59	2.105	0	0	0
	Opisthobranchia sp. 3	27.9	3.3	0.019	0	0	0
	Opisthobranchia sp. 4	856.4	101.45	0.595	0	0	0
	Peristernia forskalii	49	5.8	0.034	0	0	0
	Triviella calvariola	23.9	2.83	0.017	0	0	0
	Athleta abyssicola	36.1	4.28	0.025	0	0	0
	Athleta disparilis	0	0	0	91.7	9.9	0.043
	Athleta lutosa	0	0	0	44.1	4.76	0.021
	Athleta sp. 1	0	0	0	171.4	18.51	0.081
	Athleta sp. 2	0	0	0	125.2	13.52	0.059
	Fusinus ocellifer	17.6	2.08	0.012	0	0	0
	Neptuneopsis gilchristi	0	0	0	1409.9	152.29	0.668
	Philine aperta	3244.8	384.36	2.256	51.8	5.6	0.025
	Pleurobranchaea bubala	15129.9	1792.22	10.520	0	0	0
	White Opisthobranch	0	0	0	451.2	48.74	0.214
Porifera	Porifera sp. 1	228.1	27.02	0.159	0	0	0
	Porifera sp. 13	181.4	21.49	0.126	0	0	0
	Porifera sp. 15	776.8	92.02	0.540	0	0	0
	Porifera sp. 2	180.3	21.36	0.125	0	0	0
	Porifera sp. 4	670.3	79.4	0.466	0	0	0
	Rosella antarctica	0	0	0	515.7	55.7	0.244
	Suberites sp.	0	0	0	19232.8	2077.42	9.116
	Mycale massa	1777.8	210.59	1.236	2316.6	250.23	1.098

Phylum	Species	South Coast			West Coast		
		Total biomass (g)	Mean biomass per hectare (g/ha)	Percent (%)	Total biomass (g)	Mean biomass per hectare (g/ha)	Percent (%)
TOTAL		143821.6	17036.47	100	210987.5	22789.76	100

3.4.5. Cluster analysis

The South and West Coast surveys were combined and referred to as the Africana survey. The sub-clusters for 200 sampling sites were partitioned into 16 major groups at 5% similarity level, coloured red (4 sites – group 1), purple (18 sites – group 6), blue (3 sites – group 9), pink (6 sites – group 11), red (4 sites – group 4), orange (4 sites – group 13), green (13 sites – group 16), blue (9 sites – group 7), red (9 sites – group 15), purple (10 sites – group 5), blue (16 sites – group 3), orange (10 sites – group 10), purple (20 sites – group 12), green (14 sites – group 14), pink (19 sites – group 8) and green (41 sites – group 2) in the dendrogram (Figure 3.6). It was not possible to label Figure 3.6 with the site numbers on the horizontal axis due to lack of space.

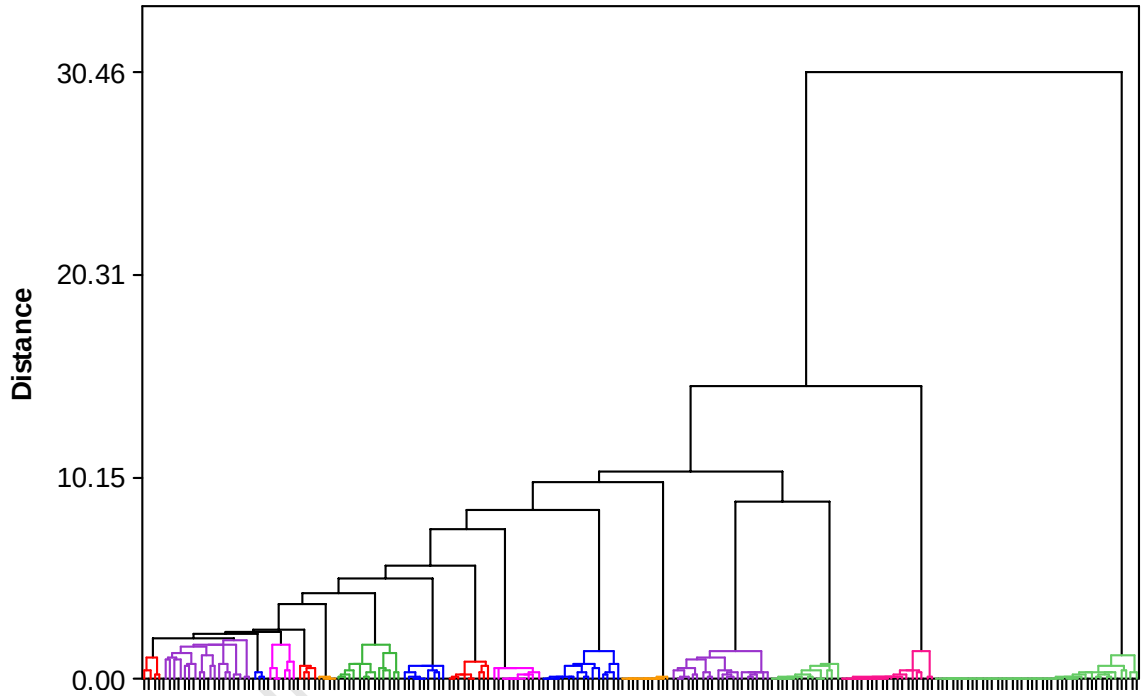


Figure 3.6. Hierarchical cluster analysis of 200 sites sampled along the South and West Coast during the Africana survey. Based on similarities by percentage species composition.

3.4.6. Comparison of the species compositions at the site groups of the Africana survey

The percentage species composition data for the benthic epifauna collected on the Africana survey were partitioned into the 16 site groups identified by cluster analysis. The percentage species compositions within each of the 16 groups are compared in Table 3.6.

The 16 groups of 200 sampling sites were characterized by different species compositions. The dominant species in group 1 in order of relative abundance were *Toraster tuberculatus*, Asteroidea (29.25%); Cnidaria sp. 2, Cnidaria (16.98%); *Sympagurus dimorphus*, Malacostraca (11.33%) and *Palinurus gilchristi*, Malacostraca (5.66%). The highest contributor of abundance in group 2 was *Sympagurus dimorphus*, Malacostraca (90.96%); followed by Cnidaria sp. 4, Cnidaria (2.01%). The

third group was dominated by *Parapagurus pilosimanus*, Malacostraca (53.36%) contributing half of the individuals collected and *Mursia cristiata*, Malacostraca (6.23%); Brittle star sp. 1, Crinoidea (5.43%) and Solasteridea, Asteroidea (3.54%) comprised the other half. In group 4 the predominant species in the samples were *Jasus lalandii*, Malacostraca (80.93%), followed by Cnidaria sp. 2, Cnidaria (9.95%) and swimming brachyura sp. 1, Malacostraca (3.31%). In group 5, more than two-thirds of the samples were represented by Solasteridea, Asteroidea (73.21%), followed by Crinoidea sp. 10, Crinoidea (9.70%) and *Sympagurus dimorphus*, Malacostraca (2.48%). The majority of invertebrates in group 6 were comprised of Polychaeta sp. 6, Polychaeta (18.59%); Holothuroidea sp 4, Holthuroidea (17.33%); Solateridea, Asteroidea (7.69%) and *Pleurobranchaea bubala*, Gastropoda (5.88%). Three species represented over two-thirds of the samples in group 7: *Spatangus capensis*, Echinoidea (53.22%); *Toraster tuberculatus*, Asteroidea (7.30%) and *Pterygosquilla armata*, Malacostraca (6.86%). In group 8, *Pterygosquilla armata*, Malacostraca (76.03%); collectively contributed over three-quarters of the number of invertebrates counted. The dominant species in group 9 were Asteroidea sp. 26, Astroidea (42.15%); Solasteridea, Asteroidea (12.18%) and *Sympagurus dimorphus*, Malacostraca (9.42%). Group 10 was dominated by one species *Suberites* sp., Porifera (95.68%). Group 11 was characterised by only one major species, *Brisaster capensis sp.,* Echinoidea (95.15%). Three species comprised over half of the samples in group 12, *Astropecten irregularis*, Asteroidea (41.68%); Asteroidea sp. 36, Asteroidea (7.26%) and *Mursia cristiata*, Malacostraca (5.25%). There were two major contributors to group 13 *Rochinia hertwigi*, Malacostraca (39.33%), *Echinus gilchristi*, Echinoidea (32.3%), *Parapagurus pilosimanus*, Malacostraca (3.75%) and Cnidaria sp. 3, Cnidaria (2.43%). *Pleurobrachaea bubala*, Gastropoda (71.9%), *Actinoptilum molle*, Holothuroidea (3.41%) and *Mursia cristiata*, Malacostraca (3.23%) made up group 14. One half of group 15 consisted of *Echinus gilchristi*, Echinoidea (50.66%) while the other half comprised mainly *Mursia cristiata*, Malacostraca (6.75%), *Astropecten irregularis*, Asteroidea (5.73%), *Pleurobranchaea bubala*, Gastropoda (4.41%) and *Achaeopsis thomsoni*, Malacostraca (3.08%). In the final group, group 16, *Mursia cristiata*, Malacostraca (34.55%) represented a third of the community, with the rest was largely made up of *Luidia sarsa africana*, Asteroidea (7.09%), *Achaeopsis thomsoni*, Malacostraca (6%), *Pleurobranchaea bubala*, Gastropoda (5.09%) and *Echinus gilchristi*, Echinoidea (4.73%).

Table 3.6. Percentage species compositions (%) of the benthic epifauna at the 16 site groups on the Africana survey differentiated by the cluster analysis.

		Percentage composition for each group/community.															
Phylum	Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Annelida	*Euphrosine* sp.	-	<0.1	1.59	-	<0.1	0.31	-	-	-	-	-	0.22	0.19	0.25	1.03	0.18
	Polychaeta sp. 2	-	<0.1	0.37	-	-	-	-	-	-	-	-	-	-	-	-	-
	Polychaeta sp. 6	-	-	-	-	-	18.59	-	-	-	-	-	-	-	-	-	-
Arthropoda	*Solenocera algoensis*	-	<0.1	-	-	-	-	-	0.51	-	<0.1	-	-	-	-	-	-
	Achaeopsis spinulosus	-	<0.1	0.61	-	-	0.24	-	-	-	-	0.20	0.89	0.37	-	0.29	3.45
	Achaeopsis thomsoni	-	<0.1	2.99	-	0.48	0.86	0.43	<0.1	3.14	-	0.54	4.84	1.12	0.93	3.08	6.00
	Agononida incerta	-	-	-	-	0.11	-	-	-	-	-	-	-	-	-	-	-
	Anomura sp. 1	-	-	-	-	-	-	-	-	-	-	-	0.11	-	<0.1	-	-
	Anomura sp. 7	-	<0.1	-	-	-	-	-	-	-	-	-	-	-	-	0.15	-
	Brachyura sp. 1	-	-	0.43	-	-	-	-	-	-	-	-	-	-	-	0.15	-
	Dardanus arrosor	-	-	-	-	-	-	-	-	-	-	-	0.67	-	0.31	-	-
	Dromidia hirsutissima	-	-	-	-	-	<0.1	-	-	-	-		-	-	-	0.15	-
	Exodromidia spinosa	1.89	0.16	-	-	<0.1	<0.1	0.43	1.08	0.90	0.35	<0.1	-	-	-	-	-
	Homola barbata	-	<0.1	<0.1	-	-	1.18	-	-	-	-	<0.1	0.45	-	-	0.29	0.36
	Macropodia formosa	-	<0.1	0.37	-	-	-	-	-	-	-	-	1.35	0.37	<0.1	0.15	0.73
	Merhippolyte calmani	-	-	0.12	-	0.26	<0.1	-	-	-	-	-	0.56	0.56	-	-	-
	Mursia cristiata	-	0.22	6.23	-	0.15	1.49	1.29	<0.1	0.90	<0.1	0.40	5.25	2.25	3.23	6.75	34.65
	Ovalipes iridescens	-	-	0.49	-	-	-	-	-	-	-	-	-	0.56	-	-	0.36
	Palinurus gilchristi	5.66	<0.1	0.24	0.14	-	0.47	2.58	-	-	-	-	0.11	-	<0.1	1.03	0.55
	Pseudodromia rotunda	-	0.11	0.24	-	-	0.78	-	-	-	-	<0.1	1.23	1.69	0.19	0.29	2.36
	Pseudodromia rotunda sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	<0.1	-	0.18
	Swimming brachyura sp. 1	-	<0.1	-	3.13	-	-	-	0.59	0.45	0.15	0.32	-	-	-	-	-
	Ovalipes punctatus	-	-	-	-	-	0.47	-	-	-	-	0.10	0.22	-	0.93	-	0.73
	Plesionika martia	-	-	0.31	-	0.67	0.39	-	<0.1	-	-	-	-	-	-	-	-
	Paracilicaea clavus	-	<0.1	-	-	-	<0.1	-	-	-	-	-	-	-	-	-	-
	Rocinela granulosa	-	<0.1	<0.1	-	-	-	0.86	-	-	-	-	0.11	0.19	0.19	0.59	0.73

Phylum	Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
	Pterygosquilla armata	1.89	0.70	-	1.36	0.70	<0.1	6.86	76.0	0.90	2.94	0.20	0.11	-	-	-	1.45
	Geryon sp.	-	-	-	-	0.81	2.20	-	-	-	-	-	-	-	-	-	-
	Goneplax rhomboides	-	-	-	-	-	0.24	-	-	-	-	<0.1	3.80	-	0.81	0.44	3.09
	Pentacheles validus	-	<0.1	0.49	-	0.59	<0.1	-	<0.1	1.35	-	-	-	-	-	-	-
	Rochinia hertwigi	-	<0.1	2.50	-	0.70	0.24	-	<0.1	-	-	-	0.22	39.3	0.31	1.17	0.73
	Scyllarides elisabethae	-	-	-	-	-	-	-	-	-	-	-	0.45	-	-	0.29	-
	Pallenopsis capensis	-	<0.1	0.12	-	-	1.02	-	-	-	-	-	3.69	0.19	-	0.29	0.55
	Parapallene algoae	-	-	<0.1	-	-	0.47	-	-	-	-	-	0.34	-	-	-	-
	Cardisoma carnifex	-	-	-	-	-	-	-	-	-	-	-	0.11	-	0.12	-	-
	Funchalia woodwardi	-	-	0.24	-	0.22	1.57	-	<0.1	-	<0.1	<0.1	-	0.37	-	-	-
	McPherasoni crab	-	-	-	-	<0.1	0.31	-	-	-	-	-	-	-	-	-	-
	Parapaguris pilosimanus	1.89	0.19	53.36	-	1.63	0.63	-	-	7.62	-	-	1.12	3.75	0.87	-	0.18
	Sympagurus dimorphus	11.33	90.96	0.73	-	2.48	0.55	-	<0.1	9.42	<0.1	0.54	1.68	0.19	-	0.29	-
	Chaceon quinquedens	-	-	-	-	<0.1	1.96	-	-	-	-	-	-	-	-	-	-
	Diogenes brevirostris	-	-	-	-	-	-	-	-	-	-	-	-	-	0.50	-	0.36
	Jasus lalandii	-	<0.1	-	80.93	-	-	-	0.43	0.45	<0.1	-	-	-	-	-	-
Ascidiacea	Ascidiacea sp. 1	-	-	<0.1	-		-	-	-	-	-	-	-	-	1.24	1.17	1.27
	Ascidiacea sp. 2	-	-	-	-		-	-	-	-	-	-	0.11	0.37	-	-	0.36
	Ascidiacea sp. 4	-	-	-	-		0.16	-	-	-	-	-	0.11	-	-	-	-
	Ascidicea sp. 10	-	<0.1	<0.1	-		0.16	-	-	-	-	-	-	-	-	-	-
Bryozoa	Bryozoa sp. 1	-	-	-	-		-	-	<0.1	-	<0.1	-	-	-	-	-	-
	Bryozoa sp. 2	-	<0.1	-	-		0.31	-	-	-	-	-	0.11	-	-	-	-
	Bryozoa sp. 3 (pink bryozoan)	-	-	-	-		0.16	-	-	-	-	-	-	0.19	-	-	-
Cnidaria	*Actinoptilum molle*	0.94	-	-	-		0.31	-	1.14	-	-	-	2.12	-	3.41	-	0.55
	Seapen sp. 2	-	<0.1	-	-		-	-	-	-	-	-	0.11	0.19	-	-	-
	Coral sp. 11	-	-	-	-		0.47	-	-	-	-	-	-	0.37	-	-	-
	Coral sp. 7	-	-	-	-		0.39	-	-	-	-	-	-	-	-	0.29	-
	Hydrozoa sp. 1	-	<0.1	0.18	-		0.39	-	-	-	-	-	-	-	-	-	-

Phylum	Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
	Hydrozoa sp. 12	-	-	-	-	-	-	-	-	-	-	-	0.11	-	<0.1	-	-
	Hydrozoa sp. 2	-	<0.1	0.24	-	-	0.31	-	-	-	-	-	-	-	-	0.15	0.18
	Hydrozoa sp. 20	-	-	-	-	-	-	0.86	-	-	-	-	-	-	-	-	-
	Hydrozoa sp. 3	-	-	-	-	-	<0.1	-	-	-	-	-	-	0.19	0.12	0.15	-
	Hydrozoa sp. 8	-	<0.1	-	-	-	<0.1	-	-	-	-	-	-	0.19	-	-	-
	Cnidaria sp. 1	3.77	0.12	0.85	-	0.59	5.02	-	-	2.24	-	-	-	-	-	-	-
	Cnidaria sp. 2	16.98	0.15	1.04	9.95	0.89	0.47	-	<0.1	0.90	-	-	1.35	0.75	-	-	-
	Cnidaria sp. 3	-	<0.1	1.34	-	<0.1	<0.1	0.43	-	-	-	0.15	2.35	2.43	-	0.29	1.82
	Cnidaria sp. 4	-	2.01	<0.1	-	0.52	0.39	2.58	-	-	-	-	0.56	0.37	-	-	-
Echinodermata	Asteroidea sp. 12	-	<0.1	<0.1	-	-	-	-	-	-	-	-	-	-	-	0.15	-
	Asteroidea sp. 18	-	<0.1	-	-	-	-	-	-	-	-	-	-	-	-	0.15	-
	Asteroidea sp. 22	-	-	<0.1	-	-	<0.1	-	-	-	-	-	-	-	-	-	-
	Asteroidea sp. 26	-	-	-	-	-	-	-	-	-	-	-	0.11	-	-	0.29	-
	Asteroidea sp. 36	-	0.75	1.53	-	1.85	2.20	-	0.22	42.15	-	-	7.26	0.19	-	-	-
	Asteroidea sp. 6	-	-	<0.1	-	-	0.39	-	-	-	-	-	-	0.19	-	-	-
	Asteroidea sp. 7	0.94	<0.1	1.04	-	-	0.16	-	<0.1	-	-	-	-	0.19	-	-	0.18
	Marthasterias glacialis	-	-	<0.1	-	-	1.10	-	-	-	-	-	1.68	-	0.50	2.79	1.09
	Persephonaster agassizi	1.89	0.26	1.34	-	0.59	1.02	2.15	<0.1	7.17	<0.1	-	-	1.87	<0.1	2.06	0.55
	Luidia sarsi africana	-	0.26	1.16	-	<0.1	1.88	-	-	0.45	<0.1	0.15	1.68	0.94	0.87	1.62	7.09
	Asteroidea sp. 35	4.72	<0.1	0.12	-	0.33	0.55	-	-	-	-	<0.1	0.11	0.19	-	-	-
	Toraster tuberculatus	29.25	0.40	2.20	-	0.30	1.02	7.30	0.26	0.45	<0.1	0.20	0.67	0.75	1.92	1.62	3.27
	Odontaster australis	2.83	<0.1	-	-	-	<0.1	-	<0.1	-	-	<0.1	-	-	-	-	-
	Pteraster capensis	-	-	-	-	-	<0.1	-	-	-	-	-	0.11	0.56	0.12	1.62	-
	Pteraster capensis sp.	-	-	-	-	-	-	-	-	-	<0.1	<0.1	-	-	-	-	-
	Astropecten irregularis	4.72	0.42	2.20	-	0.44	3.92	4.29	<0.1	4.93	<0.1	0.12	41.68	0.94	2.54	5.73	3.27
	Blue astropecten	-	<0.1	-	0.27	-	-	2.15	0.40	-	<0.1	0.42	0.11	-	-	-	-
	Calliaster acanthodes	-	-	0.37	-	-	-	-	-	-	-	-	-	-	-	-	0.18
	Solasteridae	0.94	0.42	3.54	-	73.21	7.69	-	3.81	12.18	<0.1	<0.1	0.34	0.37	0.37	0.44	2.36

Phylum	Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
	Crinoidea sp. 10	0.94	-	0.18	-	9.70	-	0.43	-	-	-	-	-	-	-	-	-
	Crinoidea sp. 11	1.89	<0.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Crinoidea sp. 200	-	-	-	-	0.74	-	-	-	-	-	-	-	-	-	-	-
	Urchin sp. 1	-	-	-	-	-	-	-	-	-	<0.1	-	-	-	-	-	-
	Echinus gilchristi	-	0.11	0.31	-	-	1.41	1.29	-	-	<0.1	-	0.67	32.30	1.61	50.66	4.73
	Stereocidaris excavat	-	<0.1	<0.1	-	-	0.39	-	-	-	-	-	-	0.19	-	0.15	-
	Brisaster capensis	-	-	-	-	-	0.63	-	-	-	-	-	-	-	-	-	0.18
	Brisaster capensis sp.	0.94	0.10	0.85	-	-	-	0.43	<0.1	1.79	<0.1	95.15	0.45	-	0.12	1.03	-
	Spatangus capensis	0.94	0.29	0.24	-	-	4.47	53.22	<0.1	0.45	0.30	0.17	0.22	-	2.92	1.76	0.73
	Holothuroidea sp. 4	-	-	-	-	-	17.33	-	-	-	-	-	-	0.19	-	-	-
	Brittle star sp. 1	-	0.33	5.43	-	<0.1	1.25	-	-	-	-	-	1.23	0.56	-	-	0.91
	Ophiuroidea sp. 2	-	-	-	-	-	-	-	-	-	-	-	-	0.19	-	1.03	-
	Ophiuroidea sp. 5	-	-	0.31	-	-	-	-	-	-	-	-	-	-	-	0.73	-
	Gorgonocephalus eucnemis	-	<0.1	0.24	-	-	0.86	0.86	-	-	-	<0.1	0.56	1.50	1.92	0.15	0.73
	Henricia abyssalis	-	<0.1	<0.1	-	-	<0.1	-	-	-	-	-	0.11	-	-	-	-
	Pseudarchaster tesselatus	0.94	0.17	0.18	0.54	1.04	<0.1	-	0.85	0.90	0.11	0.32	0.11	0.19	-	0.15	0.36
	Pseudocnella insolens	-	<0.1	<0.1	-	-	1.25	-	-	-	-	-	-	0.37	1.18	0.15	3.09
Mollusca	Opisthobranch sp. 40	0.94	<0.1	-	-	-	0.16	0.43	<0.1	-	-	-	-	-	-	-	-
	Opisthobranch sp. 41	-	<0.1	-	-	-	-	-	-	-	<0.1	-	-	-	-	-	-
	Opisthobranchia sp. 1	-	-	0.18	-	-	<0.1	-	-	-	-	-	0.34	0.19	-	1.62	-
	Opisthobranchia sp. 2	-	<0.1	-	-	-	<0.1	-	-	-	-	-	0.11	-	0.19	0.59	1.64
	Opisthobranchia sp. 3	-	0.35	0.12	-	-	-	-	-	-	-	-	-	-	-	-	0.18
	Opisthobranchia sp. 4	-	<0.1	0.67	-	-	<0.1	-	-	-	-	-	-	0.19	-	0.44	0.91
	Triviella calvariola	-	<0.1	-	-	-	0.16	-	-	-	-	-	-	-	-	-	-
	Amalda bullioides	-	<0.1	-	-	<0.1	-	-	-	-	-	-	-	-	-	-	-
	Fasciolaria lugubris ugubris	-	-	0.12	-	-	-	-	-	-	-	-	-	-	-	0.15	-
	Fasciolaria sp.	2.83	<0.1	0.12	-	0.33	0.47	1.72	0.11	0.45	<0.1	<0.1	0.22	-	-	-	-
	Hastula rufopunctata	-	<0.1	-	-	-	0.16	-	<0.1	-	-	-	0.67	-	-	0.59	0.36

Phylum	Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
	Peristernia forskalii	-	<0.1	<0.1	-	-	0.16	-	-	-	-	-	1.23	-	<0.1	0.29	0.73
	Kaloplocamus ramosus	-	<0.1	-	-	-	0.31	-	-	-	-	-	0.22	0.19	-	-	0.18
	Fusitriton magellanicus	-	<0.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Dermatobranchus sp. 4	-	<0.1	-	-	-	0.24	-	-	-	-	-	1.12	-	-	-	-
	Mollusca sp. 1	-	-	<0.1	-	-	-	-	-	-	-	-	-	0.75	-	-	-
	Mollusca sp. 3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.29	0.18
	Mollusca sp. 51	-	<0.1	-	-	0.11	-	-	<0.1	0.45	-	-	-	-	-	-	-
	Philine aperta	-	<0.1	0.85	-	-	-	-	-	-	-	-	-	0.19	-	-	0.18
	White opisthobranch sp.	0.94	<0.1	0.12	0.41	-	-	2.15	<0.1	-	<0.1	<0.1	-	-	-	-	-
	Athleta abyssicola	-	<0.1	<0.1	-	-	-	-	-	-	-	-	-	-	-	-	-
	Athleta disparilis	-	-	-	-	-	-	-	<0.1	-	<0.1	-	-	-	-	-	-
	Athleta lutosa	-	-	-	-	-	-	-	<0.1	-	<0.1	-	-	-	-	-	-
	Athleta sp. 1	-	-	-	-	<0.1	-	-	<0.1	0.45	<0.1	-	-	-	-	-	-
	Athleta sp. 2	-	-	-	0.68	-	-	-	<0.1	-	-	-	-	-	-	-	-
	Fusinus ocellifer	-	<0.1	-	-	-	-	-	-	-	-	-	-	0.37	-	-	-
	Pleurobranchaea bubala	-	<0.1	0.49	-	-	5.88	4.29	-	-	-	0.35	3.92	0.19	71.90	4.41	5.09
	Neptuneopsis gilchristi	-	<0.1	-	-	-	-	0.43	-	-	-	-	-	-	-	-	-
Porifera	*Suberites* sp.	-	<0.1	-	2.59	-	-	-	13.76	-	95.68	<0.1	-	0.19	-	-	-
	Rosella antarctica	-	<0.1	-	-	-	<0.1	3.43	-	-	-	-	-	-	-	-	-
	Porifera sp. 1	-	<0.1	-	-	-	0.24	-	-	-	-	-	-	-	-	-	-
	Porifera sp. 13	-	-	-	-	-	<0.1	-	-	-	-	-	-	-	-	0.15	-
	Porifera sp. 15	-	<0.1	-	-	-	-	-	-	-	-	-	-	-	-	0.15	-
	Porifera sp. 2	-	-	-	-	-	0.55	-	-	-	-	-	0.11	-	-	-	-
	Porifera sp. 4	-	-	-	-	-	<0.1	-	-	-	-	-	-	-	-	0.44	-
	Mycale (Mycale) massa	-	<0.1	-	-	-	<0.1	-	-	-	-	<0.1	0.56	-	-	0.15	1.09

3.4.7. Relationships between species diversity and environmental variables

As with the data in Chapter 2, it was not possible to perform an ANOVA to compare the mean species diversity indices and the mean values of the physico-chemical variables across the groups of sampling sites clustered by similar species compositions. See Chapter 2.5.8.

3.4.8. Multiple linear regression analysis for the Africana West and South Coast surveys combined

Logarithmic (log_{10}) transformation of species richness, depth, salinity, temperature, and a squared transformation of DO, were used to normalize these variables, reflected by the dome shaped frequency distribution histograms (Figure 3.7).

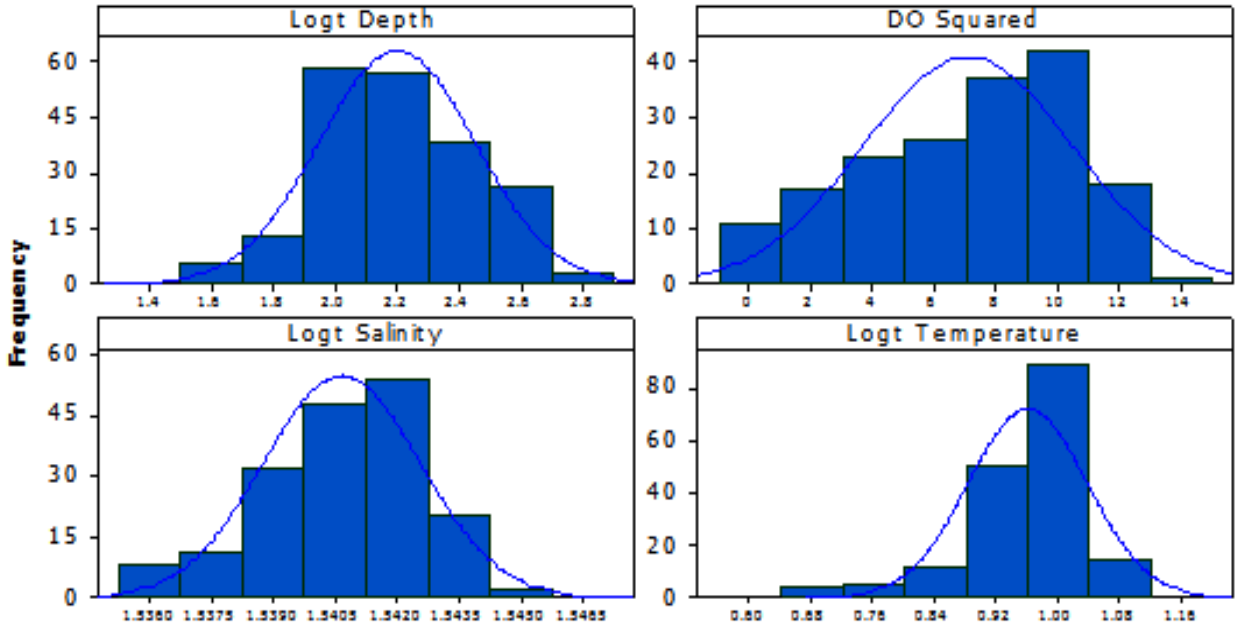


Figure 3.7. Normalization of environmental variables collected during the Africana surveys.

A matrix of Pearson's correlation coefficients was computed to identify the strengths of the relationships between species richness and the environmental variables (depth, DO, salinity and temperature) collected during the Africana surveys (Table 3.7). Logt species richness was positively correlated with depth and negatively correlated with salinity and temperature at $p < 0.05$. There were significant correlations among Logt Depth, DO Squared and Logt Salinity, which indicated collinearity between the environmental variables.

Table 3.7. The correlation matrix determined for the Africana surveys.

	Logt Species Richness	Logt Depth	DO Squared	Logt Salinity
Logt Depth	0.305*			
DO Squared	0.244	0.157*		
Logt Salinity	-0.164*	-0.841*	0.087	
Logt Temperature	-0.174*	-0.830*	-0.053	0.955*

* Significant at $p < 0.05$

Multiple linear regression analysis was performed using the combined data from the South Coast and West Coast surveys. Logt species richness was initially predicted using eight environmental variables (Table 3.8); however, the statistical inferences based on the t tests for the significance of the regression coefficients were compromised by collinearity between salinity and temperature, and between sand and sand and mud, indicated by VIF > 5.

Table 3.8. Prediction of Logt species richness using eight predictor variables for the combined Africana West and South Coast surveys.

Predictor	β Coefficient	SE	t	p	VIF
Intercept	142.880	6.080	2.38	0.019*	
Coast	0.298	0.059	5.01	<0.001*	3.447
Logt Depth	0.471	0.136	3.47	0.001	4.556
DO2	-0.004	0.007	-0.52	0.604	2.235
Logt Salinity	-94.090	39.400	-2.39	0.018*	21.950
Logt Temperature	1.939	0.823	2.35	0.020*	15.828
Sand	-0.036	0.091	-0.40	0.691	8.157
Sand and Mud	-0.107	0.094	-0.11	0.909	8.316
Mud	-0.130	0.142	-0.93	0.360	1.751
D-W	1.386*				
Critical D-W	1.670				
Adjusted R2	21.5%				

* Significant at $p < 0.05$

New predictor variables were constructed by addition of the collinear variables, specifically Logt Salinity + Logt Temperature, and sand + sand and mud (Table 3.9). Collinearity was eliminated indicated by VIF < 5. In the absence of collinearity, using six predictor variables, Coast and Logt Depth were significant predictors of Logt species richness at $p < 0.05$. The inferences were that the sampling sites on the South Coast were, on average, predicted to have higher species richness than the West Coast sites, and that Logt species richness increased in proportion to Logt Depth. However, the R^2 value of 19.5% reflected that the effects of the variance in Coast and Logt Depth on the variance in Logt species richness was relatively small. Autocorrelation was significant, indicated by the low D-W statistic, which was less than the critical value. The cause appeared to be the cyclic patterns in Logt species richness across the time-series of sampling, which could not be eliminated. The implications of autocorrelation were that the predictive precision of the model was low, and that 95% confidence intervals could not be accurately computed to determine the precision of the predicted values.

Table 3.9. Prediction of Logt species richness for the Africana surveys using six predictor variables.

Predictor		β Coefficient	SE	t	p	VIF
Intercept		-0.792	1.158	-0.68	0.495	
Coast		0.230	0.055	4.32	<0.001*	2.701
Logt Depth		0.558	0.128	4.35	<0.001*	3.972
DO2		-0.008	0.007	-1.16	0.248	2.072
Logt Salinity + Logt Temperature		0.179	0.382	-0.47	0.639	3.472
Sand + Sand and Mud		-0.023	0.092	-0.26	0.798	1.721
Mud		-0.142	0.143	-0.99	0.320	1.732
D-W	1.293*					
Critical D-W	1.682					
Adjusted R2	19.5%					

* Significant at $p < 0.05$

The significant predictor of the species richness indices at $p < 0.05$ was the geographical location of the sampling sites. The species richness was consistently predicted to be higher on the South Coast than on the West Coast, while Logt species richness was predicted to increase with respect to depth. Figure 3.8 illustrates the relationships between the species richness and depth stratified with respect to the two survey locations. The upward sloping linear regression lines comparing the relationships between species diversity and depth on the South and West Coasts were almost parallel, indicating that the patterns of increase in diversity with respect to depth were generally similar for both regions. (check if theres a diff paragraphs that goes here in the stats report)

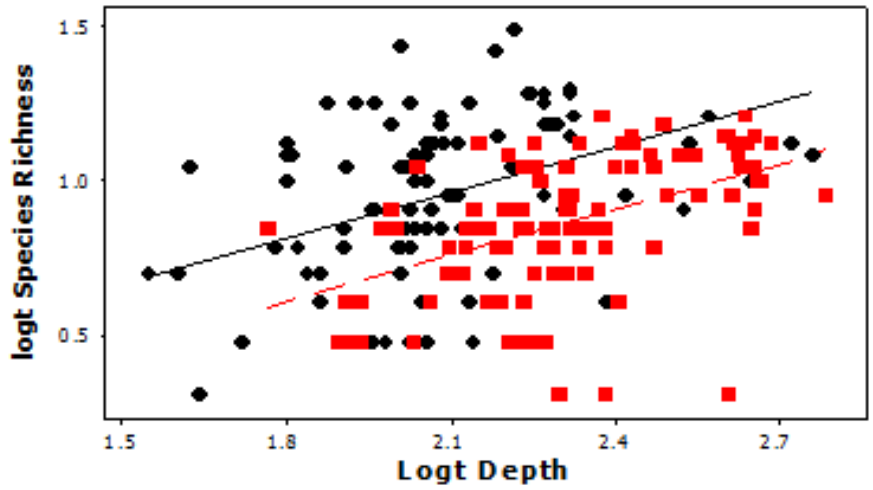


Figure 3.8. Relationships between the combined species richness of the benthic epifauna and depth for the South and West Coast surveys. South Coast sites represented by the black dots and West Coast ones by red dots.

3.5. Discussion

3.5.1. Biomass and species richness

In this study the abundance values separated out with the primary distinction occurring between the West and South Coasts, with the West Coast displaying a higher biomass and lower species richness than the South Coast (Tables 3.3 and 3.5). The difference between these two regions may be due to the cold water Benguela Current running along the West Coast, and the periodic upwelling events that are a key feature of this area, while the South Coast is characterised by a much warmer Agulhas Current. These hydrological variables, among others, have been shown (Gage, 2001) to affect community composition. For example, the benthic community may be dominated by suspension feeders that require a flow regime rich in suspended particles (Gage, 2001). Interestingly, in this study the crustaceans *Sympagurus dimorphus* and *Parapagurus pilosimanus*, both suspension feeders (R. Lemaitre, pers. comm.), were found to be key species in communities inhabiting both the South and West Coasts (groups 2, 3, 5, 9 and 13).

For the South Coast, Crustacea (Malacostraca), Mollusca (Gastropoda) and Echinodermata (Echinoidea) were the major contributors to biomass, while the West Coast was dominated by Crustacea (>40% Malacostraca), and to a lesser extent Porifera (Demospongiae) and Echinodermata (Asteroidea). It is interesting to note that along both coasts the largest contributor to biomass were Crustacea (Malacostraca), although species composition differed for each coast. Gage (2001) noted that the composition of the benthic community is broadly similar at similar depths; however, when comparing the community composition of this study, with that of other studies (De Léo and Pires-Vanin, 2006; Brandt and Ebbe, 2009), different depths appear to be dominated by different taxa. On the Brazilian South East shelf Crustacea were the dominant group, followed by Mollusca, Echinodermata and then Polychaeta (De Léo and Pires-Vanin, 2006), this dominance pattern is similar to that of the South African South Coast communities (Table 3.3). This similarity could be attributed to the fact that both the South African South Coast and Brazilian South East shelf are dominated by western boundary currents, which carry warm subtropical waters along the coast (Stramma *et al.*, 1990; Podesta *et al.*, 1991), and therefore species with similar environmental requirements will dominate these regions, such as the suspension feeders mentioned previously.

Surveys conducted in the Pacific (Mair *et al.*, 2009) and the Brazilian South East shelf (De Leo and Pires-Vanin, 2006) found that Crustacea had the highest number of species: 61 species. This value is much higher than the values found in this study (South Coast: 26 species in total, 3.6 species per trawl; West Coast: 19 species in total, 2.9 species per trawl), even when the samples from the two coasts were combined. Echinodermata, in accordance with Mair *et al.,* (2009; 28 species), displayed the second highest number of species, with 26 species overall (4.3 species per trawl) on the South Coast and 21 species in total (3.4 species per trawl) on the West Coast. Mollusca, however, had slightly lower numbers of species in this study (South Coast: 17 species in total, 1.4 species per trawl; West Coast: 13 species overall, 0.7 species per trawl) when compared to the Western Mediterranean

study by Cartes *et al.,* (2009; 21 species), and the Brazilian South East shelf study by De Leo and Pires-Vanin (2006), in which 11 species were collected.

Depth was the main determining factor of species richness on both the West and South Coasts (Table 3.9). This is in agreement with other studies conducted on the continental shelf of Brazil (Pires, 1992), the Gulf of Carpentaria, Australia (Long *et al.*, 1995), the western Gulf of Mexico (Escobar-Briones and Soto, 1997), the Galician continental shelf and upper slope of Northwest Spain (Farina *et al.*, 1997), the Brazilian South East shelf (De Léo and Pires-Vanin, 2006), the Spermonde Archipelago, Indonesia (Cleary *et al.,* 2005) and the West Antarctic Peninsula continental shelf (Glover *et al.*, 2008). The general distribution patterns of the benthic macroinvertebrates are in agreement with previous worldwide studies regarding their well pronounced depth-dependency and spatial heterogeneity (Pires, 1992; Long *et al.*, 1995; Escobar-Briones and Soto, 1997; Farina *et al.*, 1997; Pires-Vanin, 2001; De Léo and Pires-Vanin, 2006; Glover *et al.*, 2008). Although depth has been demonstrated as the main variable controlling the zonation of deep-sea assemblages in this study, the final environmental factors or mechanisms have not been determined.

The study by Caranza *et al.,* (2008), on the Uruguayn and northern Argentinean shelf, confirmed a strong effect of environment in the distribution patterns and assemblage structure of megabenthic gastropods. They found number of species and diversity to be correlated with changes in bottom-water oxygen concentrations (Carney, 2005) and sediment-bound pigments (Carney 2005). De Léo and Pires-Vanin (2006) also found that megafaunal distribution was governed firstly by grain size, and then by depth. A similar study in the Gulf of Mexico showed that sediment mean grain size, percentage of clay and organic matter best explained the macrofauna spatial patterns, however, depth still had an overriding role in the distribution patterns of the macrofauna (Hernández-Arana *et al.*, 2003). Depth-related patterns in environmental conditions may also provide opportunity for non-interactive enhancement of species richness within areas of transition between two adjacent ecological assemblages, or ecotones (Gage, 2004). The other mechanisms most frequently proposed for distribution patterns are the lack of light (discussed below), high hydrostatic pressure, low temperature, water mass and nature of substratum (Carney, 2005). It has also been suggested that annual resource stability and the food supply to the seafloor can account for diversity patterns (Corliss *et al.*, 2009).

The main impact of depth on community structure is reduction in light levels, particularly over the first 100 - 200 m, below these depths other environmnetal factors play larger roles (i.e. temperature, carbon). Depth covariates with so many other oceanographic properties, including pressure, that identifying a causal factor from surveys may be almost impossible. The reduction in light influences primary productivity, which in turn is influenced by nutrients (Renema, 2002). Light penetration is also influenced by turbidity, for example light will invariably be lower in areas with high fluvial influx, due to higher concentrations of inorganic and organic particles, coupled with increased planktonic abundance (Hallock, 1988; Renema, 2002). All these particles filter down to the deep sea as organic matter, which acts as food for the macroinvertebrates. Benthic ecosystems in the deep sea are dependent on this detrital flux of organic carbon sinking from the euphotic zone for their survival

(Clarke, 1985; Gage and Tyler, 1991; Arntz *et al.*, 1994; Glover *et al.*, 2008). The spatial variability of these faunal communities is also typically linked to the quantity and quality of detritus originating from the pelagic realm (Longhurst, 1985; Graf, 1989; Smith, 1994; Ambrose and Renaud, 1995; Smith *et al.*, 1997). Supporting this link, Menot *et al*., (2009) found that the predictability of the macrofaunal response to organic enrichment varied according to depth and location. The benthos, in turn, helps to recycle the nutrients required by the planktonic algae, which supports much of the ocean's benthic and pelagic production (Graf, 1992).

In contrast, however, a recent transect study from Boston Harbour to Georges Bank found that the benthic community displayed no change in community composition with increasing depth, and furthermore that sediment grain-size could not be solely used to explain diversity patterns (Maciolek and Smith, 2009). The present study also found that sediment type could not be used to explain the community patterns observed offshore of the South and West Coasts of South Africa. A possible alternative is that their initial colonisation might have been determined by historical processes, creating isolation and extensive open niche space, leading to opportunities of colonisation after regional- or even global-scale extinction events (Simpson, 1953; Hutchinson, 1959).

3.5.2. Biogeography

Biogeographical zones are normally verified by the distribution patterns of dominant species (Field *et al.*, 1982; Turpie and Crowe, 1994), or those species whose ranges most closely fit the range identified by cluster analysis or ordination. In this study, however, there did not appear to be a clear cut boundary between the groups. The groups/communities identified in this study, through cluster analyses at a 5% similarity threshold, were found to have a species composition dominated by a single, or at most two, dominant species. Together the West Coast and South Coast were clustered into 16 communities. These 16 communities appear to have limited geographical patterns, as shown in Figure 3.8 below, even though the analyses suggest that depth has a statistically significant impact on the community patterning. Of the 16 identified communities five were restricted to the West Coast, three to the South Coast and the remaining eight were found along both West and South Coasts.

Along the West Coast group 5, characterised by the sea star Solasteridae*,* formed a deep offshore community along the 500 m isobath, while group 8, dominated by the mantis shrimp, *Pterygosquilla armata,* formed a shallow nearshore community. Group 4 represented by the West Coast rock lobster, *Jasus lalandii*, displayed a restricted distribution on the northern edge of the West Coast sampling site along the 100 m isobath. The sponge, *Suberites* sp., characterising group 10, occurred in two distinct restricted patches on the continental shelf, one to the north of the West Coast sampling region and the second further south at the 32°S latitudinal line. Group 9 was the final group limited to the West Coast, distinguished by the sea star, Asteroidea sp. 36, it displayed a small non-distinct patchy distribution.

Of the three groups limited to the South Coast region, only group 14 exhibited a restricted distribution to the East of the sampling region. This group was characterised by the nudibranch *Pleurobranchaea*

bubala. Group 15, represented by the urchin, *Echinus gilchristi*, exhibited a patchy distribution between the 200 and 500 m isobaths along the South Coast. The last group found only along the South Coast, was group 16, identified by the crab *Mursia cristiata*. Group 16 revealed a slightly patchy distribution, although it also covered a definite inshore area (Figure 3.9).

The remaining eight groups cover both the West and South Coast regions. Of these, group 2 (represented by the shallow water anemone crab, *Sympagurus dimorphus*) and group 3 (characterised by the deep water anemone crab, *Parapagurus pilosimanus*) were the most extensive, both running along the 200 m isobath, although group 3 did occur further offshore along the West Coast than along the South Coast. A small restricted group, group 13, dominated by the spider crab *Rochinia hertwigi* and the urchin *Echinus gilchristi*, occurred in two distinct places, on the continental slope along the South Coast at 32ºE and to the north of the West Coast sampling region. Group 1, which is characterised by the sea star *Toraster tuberculatus,* appears to have a small patchy distribution, limited to the transition zone, where the Benguela and Agulhas Currents meet.

Lombard *et al*., (2004), using abiotic surrogacy (temperature and depth), proposed six bioregions in the area where the current study was conducted. These were the Namaqua bioregion, the South-western Cape bioregion and the Atlantic offshore bioregion along the West Coast of South Africa, and the Agulhas bioregion, West Indian offshore bioregion and the Indo-Pacific offshore bioregion along the South Coast. This, however, is in contrast to the current study, where 16 communities were found within the same region (Figure 3.9). Within the Namaqua bioregion at least four groups/communities were found in the current study and another six were found to spread outside of this bioregion into two others, the Atlantic offshore bioregion and the South-western Cape bioregion. This pattern was also found for the Agulhas bioregion, where only two groups/communities were found within the bioregion and at least seven groups/communities overlap into other bioregions, suggesting that the boundaries of the bioregions based on abiotic variables are inaccurate for macrofaunal assemblages. At a large scale the use of abiotic variables to delimit areas is useful (Lombard *et al*., 2004), as sampling such very large regions could pose many logistical problems. This study, however, has shown that abiotic variables are not adequate at smaller scales, where the use of macrofaunal distribution data is a more accurate method to determine groups/communities, contrary to a study done by Dunstan et al. (2012). They did however, use a much greater variety of abiotic variables to delimit areas than was available for use in the current study.

Most diversity studies across coastal shelves have focused on single taxa, such as fish (Turpie *et al*., 2000; Beyers, 1994) or seaweeds (Bolton et al., 2004). The patterns of diversity can, however, differ among taxa, due to community-wide differences in dispersal ability and other taxon-specific factors (Flather *et al.*,1997; Gaston, 2000; Reyers *et al.*, 2000; Caranza *et al.*, 2008). Multi-taxon studies are therefore important in order to setup high-quality conservation strategies (Cleary *et al.*, 2005). Marine habitats are still grossly underrepresented in the protected areas network (Chape *et al.*, 2005). Hence, this offshore region is in dire need of further research in ecology and biogeography. Furthermore, biogeographic classifications, such as the present study, are essential for developing ecologically representative systems of protected areas, as required by international agreements. The

region where the current study took place needs to be sampled in a more rigid fashion, possibly using a depth-stratified design. This will ensure that an equal number of samples could be collected in each depth interval which would make it more comparable. Sampling should also be extended to the East Coast of South Africa, as this area is both severely undersampled (see Chapter 1) and likley to reveal a great many communities due to is diverse habitat types (Dingle *et al.,* 1987; Sink *et al.,* 2010).

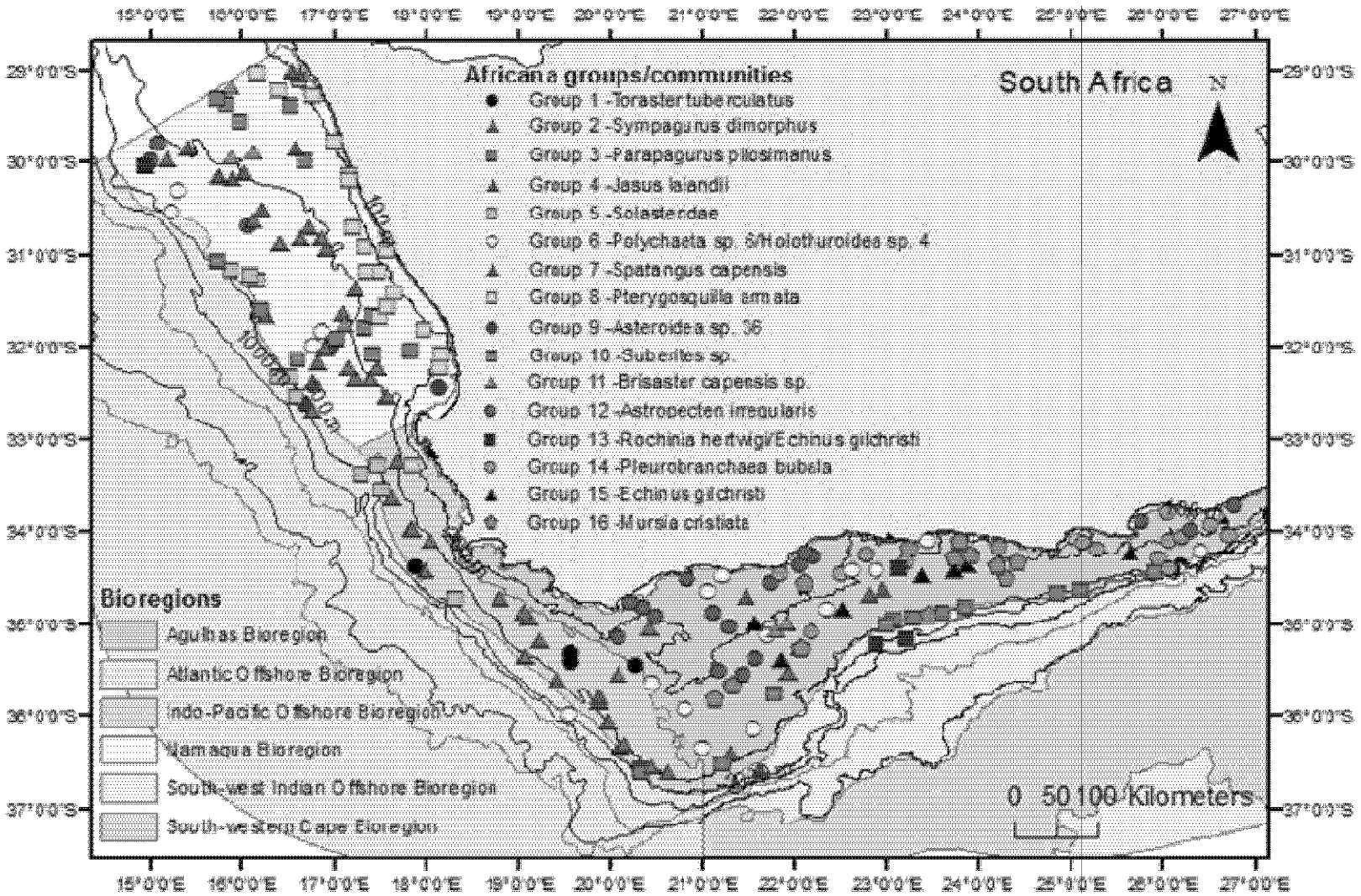


Figure 3.9. The Africana survey's 16 groups/communities identified by the cluster analysis, overlaid onto the biozones depicted in Lombard *et al.,* (2004).

Chapter 4

USING A LARGE-SCALE BIODIVERSITY DATA SET TO QUANTIFY AND INTERPRET KEY PATTERNS IN BENTHIC DIVERSITY

4.1. Introduction

Interest in biological diversity has increased in recent years in response to the recognition of the extensive damage caused to global ecosystems by the increasing scale of anthropogenic activities. For conservation purposes the number of species has traditionally been used as a surrogate for monitoring species diversity (Rosenzweig, 1995; Gaston and Spicer, 1998), although measures of diversity incorporate not only the number of different species present, but their relative abundance or numerical composition (Sanders, 1968, see also below).

Marine species diversity varies enormously at different localities, the two most widely cited gradients being those associated with latitude and with depth (Briggs, 1974). First, for many groups (e.g. Cnidaria, Mollusca, Crustacea and fishes), but not all (Clarke, 1992), diversity is considerably higher in tropical regions than in cooler regions; however, the cline from the Antarctic to the tropics is far less well established than that in the Northern Hemisphere, if it occurs at all (Gray, 1997). Exceptions include Asteroidea, which are most diverse in the cold temperate Northeast Pacific waters off Canada and the USA (Clarke, 1992). Probably the most well-known latitudinal diversity pattern in the marine domain is that of Cnidaria genera and species, which reach highest species diversity in the tropical Indo-West Pacific Ocean (especially in the area between the Philippines, Indonesia and northeast Australia), intermediate diversity in the East Pacific and West Atlantic, and lowest diversity in the East Atlantic (Stehli and Wells, 1971; Norse, 1993). Across the Indian Ocean diversity decreases irregularly from the high diversity epicentre, the Indo-Pacific, dipping and then rising in the Red Sea and Africa for some groups, such as corals and fish species (Briggs, 2007). Similar patterns of irregular decreasing and increasing diversity have been shown for mangroves, corals and gastropod snails (Huston, 1994; Veron, 1995).

Another species diversity pattern that has received much attention is that associated with depth, where diversity increases from shallow regions to the deep sea (Sanders, 1968). This depth pattern has been confirmed by Grassle and Maciolek (1992) in a study along the United States East Coast. High species diversity in samples of macrobenthos of deep-sea sediments is also now well established (Gage, 1996). The current understanding is that diversity reaches a peak at about 3 000 m and then declines again in deeper waters (Rex, 1983).This generally accepted fact, however, is based on a relatively small number of studies, most of which are also taxonomically limited (Gray *et al.*, 1997). The most extensive quantitative studies are from the Pacific (e.g. Jumars, 1976) and North Western Atlantic (e.g. Grassle and Maciolek, 1992), in which most studies are restricted to a relatively small bathymetric range.

Along the South African coastline i.e. shallow nearshore and not offshore regions, Mollusca, Polychaeta, Echinodermata and Brachyura all displayed species richness patterns that adhere to a well-documented pattern, increasing from southwest to northeast. However, for Amphipoda, Isopoda, Ascidiacea and Cnidaria species richness was highest along the South Coast (Branch and Griffiths, 1988; Bustamante *et al.*, 1997; Awad *et al.*, 2002). The distribution of organisms relative to their habitat is of central importance to ecology, and provides an initial insight into the types of ecological processes that regulate populations and assemblages (Nanami *et al.*, 2005). According to Caranza *et al.* (2008), the study of the distribution of faunal assemblages will lead to better understanding of the forces that shape spatial variation in community structure and diversity, an unavoidable issue for effective conservation and management of marine biodiversity. Information about species ranges is also important in order to establish the extent of diversity at regional scales (Levin *et al.*, 2001). An analysis of species richness is particularly useful in conservation, as it can draw attention to regions of high species richness, a factor that is often considered in the selection of protected areas (Kerr, 1997). It is for this reason that this study aims to provide the first insight, for the South African offshore region, into the pattern of species richness using indices for offshore benthic invertebrates.

Species diversity is now recognised as a complex concept, which requires measures that take into account other facets of diversity, such as biodiversity (Purvis and Hector, 2000). The species richness indices all require data on species composition in the areas being studied, in contrast to trophic indices, which are based on physical and chemical parameters (Purvis and Hector, 2000). Diversity and similarity indices are used as an approach to estimate biological quality through the structure of the community, using the abundance data of a population (Danilov and Ekelund, 1999). A way to measure diversity is to focus on species evenness, which measures how evenly levels of abundance are distributed among the species (Danilov and Ekelund, 1999; Purvis and Hector, 2000). In many cases authors summarize both components, the number of species and evenness, in a single value through heterogeneous indices (Peet, 1974), such as the Shannon index H' (Shannon and Weaver, 1949) or the Simpson concentration D (Simpson, 1949).

Most diversity indices can be referred to as cardinal indices, in which species are treated equally (Magurran, 2004). Indices that attempt to weight rare species, or any other type of species, are known as ordinal indices, while diversity indices attempt to describe whole communities with one statistic (Magurran, 2004). Magurran (2004) divided diversity measurements into: (a) indices that measure the increase in species number, such as the Margalef species richness index, and (b) indices based on the proportional abundance of species that solve the increase in number of species and uniformity in a simple expression. This last category of indices can also be divided into those based on statistics, information theory and dominance indices. Indices derived from the information theory, such as the Shannon–Wiener, are based on a logical assumption: the diversity, or information in a natural system, can be measured in a similar way as information contained in a code or message (Salas *et al.*, 2006). On the other hand, dominance indices, such as the Simpson index, are referred as measurements that ponder the abundance of the most common species, rather than the increase in species number

(Salas *et al.*, 2006). Each of the various dominance and information-statistic indices may give values that are slightly different to those obtained from other indices, however, all of the values are generally well correlated (Stiling, 2002).

The Margalef index is a measure of species diversity, in which the greater the diversity the higher the index value. It is calculated from the total number of species present, and the abundance or total number of individuals (Magurran, 2004).The Shannon index (H') is an information statistic index, and assumes that all species are represented in a sample and that the sample was obtained randomly (Stiling, 2002). The most important source of error in this index is failing to include all species from the community in the sample, while an advantage of the index is that it takes rare species into account. As a result, it is often chosen for its computational simplicity. Values of the Shannon diversity index for communities typically fall between 1.5 and 3.5. The Shannon index is affected by both number of species and their equitability or evenness. A greater number of species and a more even distribution both increase diversity, as measured by H'.

Information-statistic indices are affected by both number of species recorded and their equitability or evenness. To express how evenly individuals are distributed among the different species a Pielou's evenness index was used. Ecologists are interested in the relative abundances of species (Magurran, 1988), and the term Evenness (with its reverse Dominance) is used for the numerical percentage composition of the relative abundances of species. When the species present are virtually equal in abundance i.e. display a high evenness, this is typically equated with high diversity (Magurran, 1988). Conversely, the less numerically equal the species are, the less diverse the sample is or, on the other hand, the greater the dominance in the fauna (Sanders, 1968).

Simpson's diversity index (D) is a dominance index, the greater its value the greater the sample diversity (Stiling, 2002). The index represents the probability that two individuals randomly selected from a sample will belong to different species. Disadvantages of this index include: being biased towards the most abundant species, a problem common to all dominance indices, and that the addition of rare species to a sample causes only small changes in the value of D. An advantage of this index, however, is that it is easy to calculate and interpret, and that it is regarded as more accurate and realistic than other diversity indices, such as the Berger-Parker index (Stiling, 2002).

In South Africa the Shannon index has been applied to pelagic fish assemblages (Shine, 2005), and for select invertebrate taxa along the coastline of South Africa. As a result, there is a large gap in the use of diversity indices in marine research in South Africa. Thus, the aim of this study was to look at various diversity indices (all those described above) for the benthic invertebrate assemblages along the West and South Coasts of South Africa.

A number of hypotheses have been proposed to account for changes in species diversity. Rohde (1998) listed 28 theories that specifically applied to latitudinal gradients. Zacharias and Roff (2001) states that for the latitudinal diversity hypothesis, diversity decreases with increasing latitude. This pattern holds true for many marine taxa, but there are exceptions that do not adhere to the trend

(Barbour *et al.*, 1987; Stevens, 1989; Willig *et al.*, 2003). However, latitudinal differences have not been tested for in the offshore South African benthic environment and this will be one of the facets of the present study.

Indices are very useful tools in decision-making processes, since they can be used to evaluate and assess ecological integrity, and can evaluate both the state of the ecosystem and the response of managers. They can also be used to track progress towards meeting management objectives and facilitate the communication of complex impacts and management processes to a non-specialist audience. Indices, therefore, can and should be used to help direct research, and to guide policies and environmental programs (Pinto *et al.*, 2009).

4.2. Materials and Methods

The analyses for this study are based on a series of benthic trawl surveys conducted along the South Coast and West Coast of South Africa and described in earlier chapters. It should, however, be noted that the surveys were restricted to soft surficial sediment habitats, which are thought to be relatively low in species diversity, compated to hard substrata (Gray, 1997). Three cruises were conducted: two along the West Coast (aboard the *F.R.S. Africana* and the *R/V Dr Fridtjof Nansen* respectively), and one along the South Coast (*F.R.S. Africana*). The data from the three cruises (Africana West Coast survey, Africana South Coast survey and Nansen West Coast survey) were analysed separately, as slightly different trawling gear and sampling design was employed abroad the two vessels. For more information of sampling methods and detailed descriptions of the *Dr Fridtjof Nansen* cruise along the West Coast refer to Chapter 2.3. Similarly, for information regarding the *F.R.S. Africana* cruises refer to Chapter 3.2.

4.2.1. Statistical Analyses

The computer programme MINITAB 16.1 was used to perform all the statistical analysis during this study.

4.2.2. Species area relationships

Separate species-area curves for the samples collected on the Africana South Coast, West Coast and Nansen West Coast surveys were constructed since the benthic communities were sampled with different gear. The cumulative area sampled was placed on the horizontal axis, while the cumulative number of species of benthic epifauna collected was placed on the vertical axis. Species area relationships were constructed on $\log_{10}$ transformed axes. It was expected that the log-log relationship would be approximately linear, consistent with a power function species-area model defined by $S = C A^Z$, where C = the number of species in the smallest sampling area, A = the sampling area, and Z = the slope of the species-area relationship in log-log space. Alternatively, the relationship could be defined by the semilog model S = C + Z logt A, approximating a straight line when the cumulative area was logarithmically transformed and the cumulative number of species was arithmetic (Connor

and McCoy, 1979; Scheiner, 2003). Linear regression analysis was used to determine which of these two models best fitted the data.

4.2.3. Species diversity indices

Diversity indices were computed to estimate richness, rarity and commonness of species of the benthic epifauna at the sampling sites. Diversity indices provided more information about community composition than species richness alone (i.e. the total number of species present), as they also took the relative abundances of the different species into account (Rozenweig, 1995; Begon *et al.*, 1996; Harper, 1999). Simpson's, Shannon's and Margalef's indices of diversity were computed and compared for the purposes of this study.

To calculate Simpson's diversity index (*D*), the proportion of species (*i*) relative to the total number of species (p_i) was calculated and squared. The squared proportions for each species were summed, and the reciprocal was taken:

$$D = \frac{1}{\sum_{i=1}^{s} p_i^2}$$

To calculate Shannon's diversity index (*H*), the proportion of species (*i*) relative to the total number of species (p_i) was calculated and then multiplied by the natural logarithm of this proportion ($\ln p_i$). The product was summed across species and multiplied by -1 so that the index was positive:

$$H = -\sum_{i=1}^{s} p_i \ln p_i$$

Margalef's Alpha (α) was computed using the formula:

$\alpha = (S - 1) / \ln N$

where, *S* is the number of species (i.e. the species richness), and *N* is the total number of individuals.

4.2.4. Multiple linear regression analysis

The dependent variables were the four species diversity indices (species richness, Shannon's *H*, Simpson's *D* and Margalef's Alpha), measured as continuous quantitative variables. Logarithmic ($\log_{10}$) transformation of species richness, Simpson's D, depth, salinity, temperature and a squared transformation of DO, were used to normalise the variables. A matrix of Pearson's correlation coefficients was computed to identify the strengths of the relationships between species richness, species diversity and the environmental variables (depth, DO, salinity and temperature) collected during the Africana survey and during the Nansen survey. An explanation for the method used is provided in Chapter 3, section 3.3.2.

According to Turpie *et al.* (2000) conservation 'hotspots' in terrestrial systems are usually defined as areas of peak value in terms of criteria such as species richness. Hence, the same criteria were applied for the current study in the marine environment, in which the patterns of species richness and diversity indices were examined to investigate whether any 'hotspots' could be identified for macro-invertebrates in the offshore region of South Africa.

4.3. Results

4.3.1. Species-area relationships on the Africana surveys

The species-area curves for the samples collected on the Africana South Coast, West Coast and Nansen West Coast surveys are compared in Figure 4.1. The cumulative number of species rose to an asymptote more steeply in the South Coast samples than in the West Coast samples, indicating that the species richness increased more rapidly on the South Coast than on the West Coast.

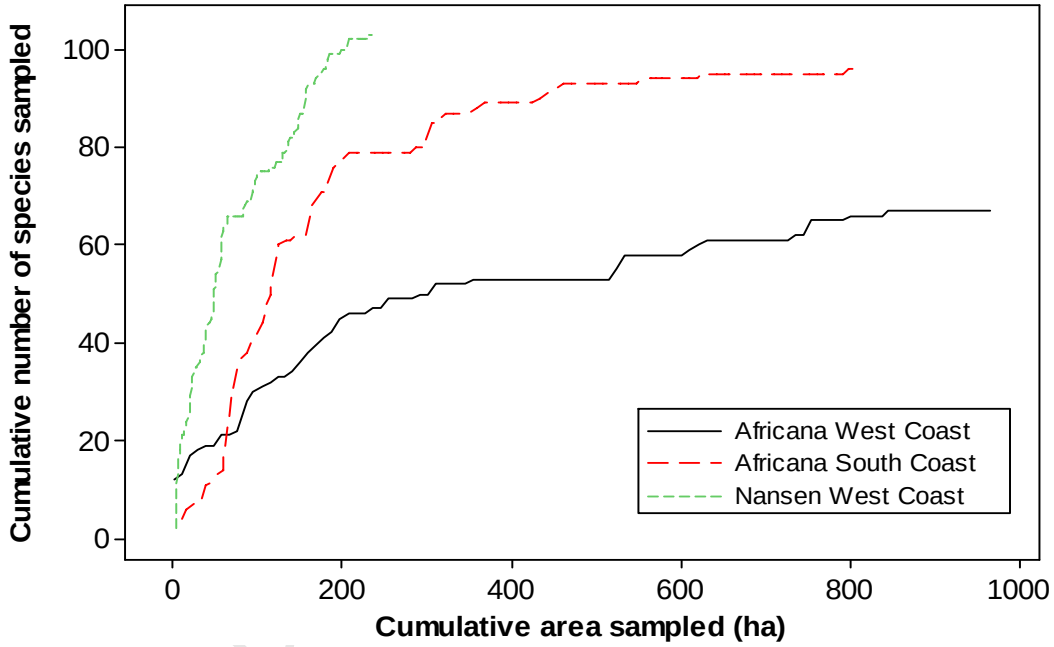
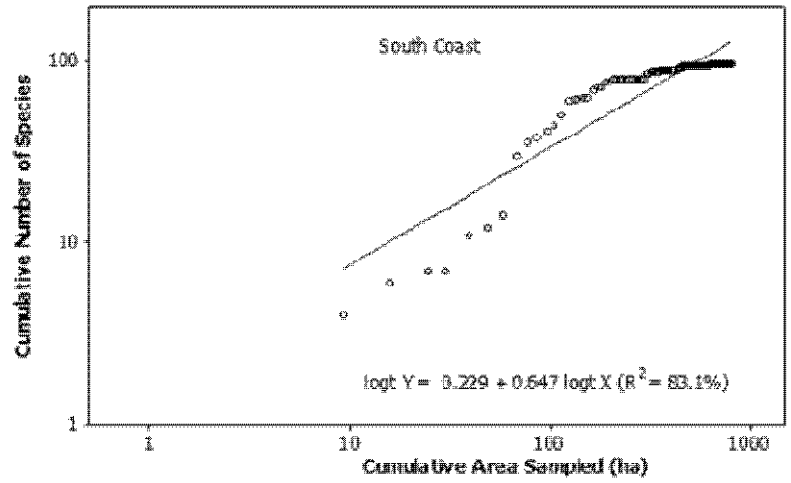


Figure 4.1. Species area curves depicting the benthic epifauna for the Africana South Coast and West Coast surveys, and the Nansen West Coast survey.

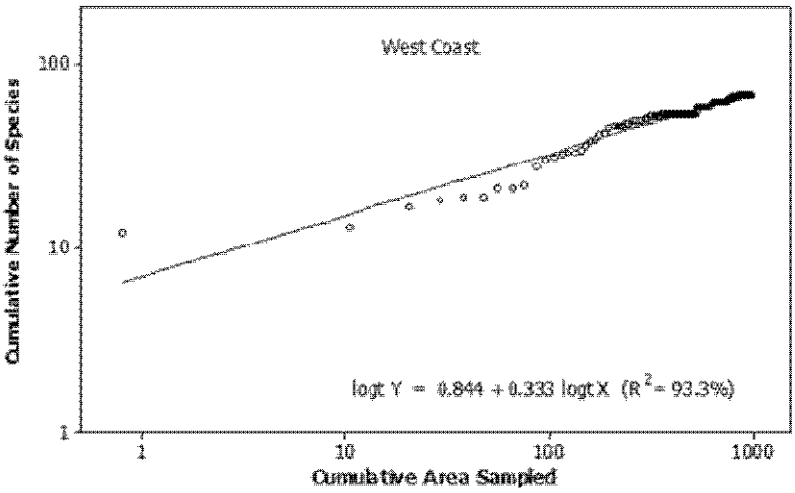
The species-area curve for the samples collected during the Nansen West Coast survey showed that the rate of species accumulation was much faster than in the Africana West Coast and South Coast surveys. Thus giving further evidence that the gears used on the Nansen survey and on the Africana survey sampled differently, and justifies the initial decision not to combine the Nansen and Africana survey data sets.

The species area relationships constructed on $\log_{10}$ transformed axes were approximately linear (Figure 4.2), consistent with a power function species-area model defined by $S = C A^Z$. Simple linear regression analysis indicated that the highest slope was $Z = 0.657$ ($R^2 = 83.1\%$, $p < 0.001$) for the

South Coast samples, and the lowest slope was Z = 0.333 (R^2 = 93.3%, p < 0.001) for the West Coast samples (Figures 4.2a and b). The Nansen West Coast had a lower slope at Z = 0.598 (R2 = 91.7, p < 0.001) (Figure 4.2c) than the Africana South Coast samples, but higher than the Africana West Coast samples, reflecting the more effective sampling methods used during the Nansen West Coast survey. R^2 represented the proportion of the variation in species diversity explained by the sampled area. It should be noted that the Nansen West Coast survey sampled a significantly smaller region that the Africana South and West Coast surveys. For the West Coast, a tenfold increase in the area of the habitat sampled (from 50 ha to 500 ha) produced a 2.8 fold increase in the number of species, from 19 to 53. For the South Coast, a similar tenfold increase in the area of the habitat sampled produced a 7.6 fold increase in the number of species, from 12 to 93. A tenfold increase in sampling area for the Nansen survey, from 20 to 200 ha produced a 3.4 fold increase in the number of species collected, from 29 to 100 (Figure 4.2c).



a)



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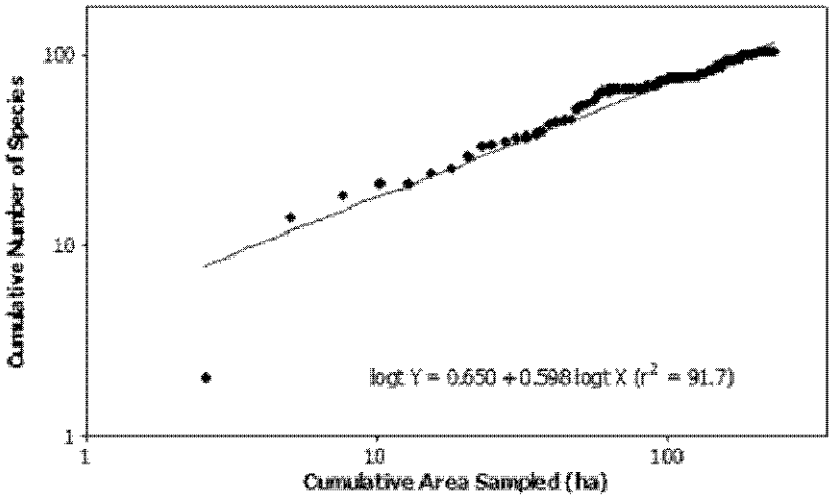

c)

Figure 4.2. Species-area curves for the a) Africana South Coast b) Africana West Coast and c) Nansen West Coast surveys using log-log axes.

4.3.2. Species diversity indices on the Africana surveys

Consistent with the species-area curves, the species diversity, measured in terms of the mean, median, minimum and maximum species richness, Shannon's H, Simpson's D and Margalef's Alpha (Table 4.1) were consistently higher in the samples from the Africana South Coast than from the Africana West Coast. The matrix plot (Figure 4.3) illustrates the relationships between the indices.

Table 4.1. Species diversity indices per trawl for the Africana and Nansen surveys.

		Species Richness	Shannon's H	Simpson's	Margalef's
Africana South Coast	Mean	10	1.534	4.081	2.404
	Median	9	1.538	3.560	2.199
	Minimum	2	0.043	1.010	0.818
	Maximum	31	2.855	13.173	6.514
	Variance	34	0.317	5.514	1.042
	Standard deviation	6	0.563	2.348	1.021
	Standard error	1	0.058	0.241	0.105
Africana West Coast	Mean	8	0.929	2.471	1.516
	Median	8	0.736	1.71	1.443
	Minimum	2	0.022	1.006	0.307
	Maximum	16	2.247	7.451	3.613
	Variance	12	0.466	2.846	0.642
	Standard deviation	4	0.682	1.687	0.801
	Standard error	0.3	0.067	0.165	0.078
Nansen West Coast	Mean	12	1.313	3.292	2.404
	Median	11	3.144	2.274	2.199
	Minimum	2	0.071	1.021	0.818
	Maximum	40	3.144	15.746	6.514
	Variance	60	0.465	6.695	2.481
	Standard deviation	8	0.682	2.587	1.575
	Standard error	1	0.069	0.260	0.158

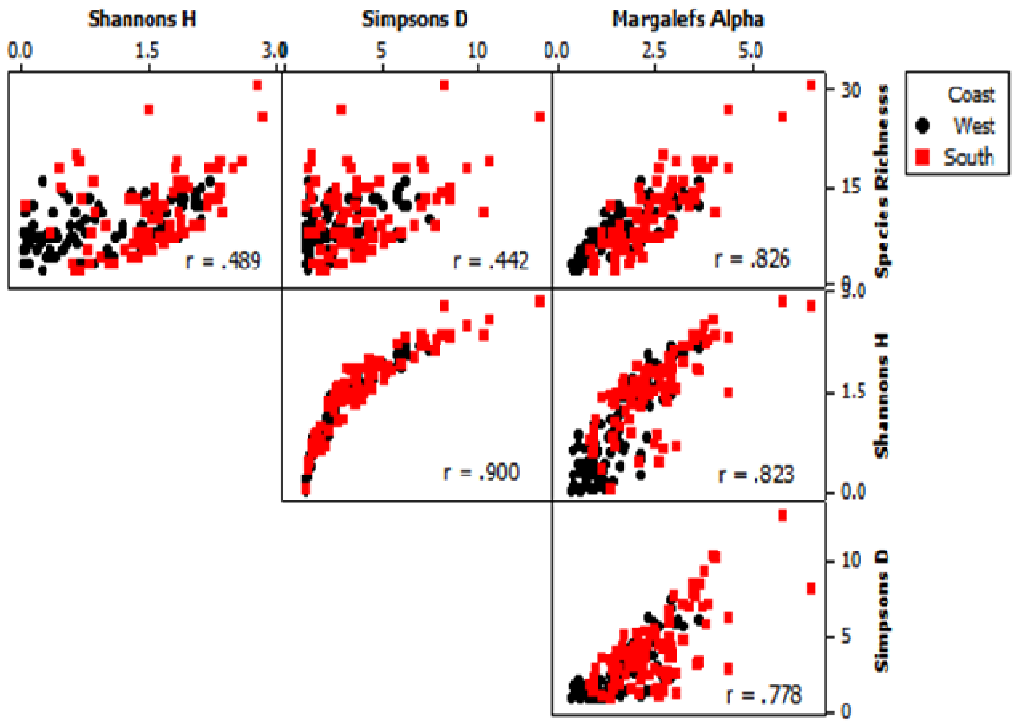

Figure 4.3. Matrix plot of species diversity indices for the Africana South Coast and West Coast surveys.

The four species diversity indices were strongly correlated with each other at $p < 0.001$ (Pearson's r = 0.442 to 0.900) as they tend to express the same information in different terms, however, the scatterplots indicated that the relationships were not entirely linear (Figure 4.3). The isolated red squares on the right hand sides of the scatter plots reflected the highest species diversities observed. mainly in samples from the South Coast.

The species diversities of the benthic epifauna, measured in terms of the mean, median, minimum and maximum species richness, Shannon's H, Simpson's D and Margalef's Alpha for the samples collected in the Nansen West Coast survey are presented in Table 4.1. All of the indices were consistently higher on the Nansen West Coast survey (Table 4.1 and Figure 4.4) than the Africana West Coast survey (Table 4.1 and Figure 4.3), indicating that the sampling methods used during the Nansen survey collected a higher diversity of species than the methods used during the Africana survey (see Table 4.1 for comparison). The Nansen West Coast survey also displayed higher mean, median and maximum species richness than the South Coast values and had the same Margalef's Alpha as the South coast (see Table 4.1 for comparison). Non-linear relationships were observed between the indices computed from the Nansen West Coast survey, consistent with the results obtained for the Africana West Coast survey (Figure 4.4).

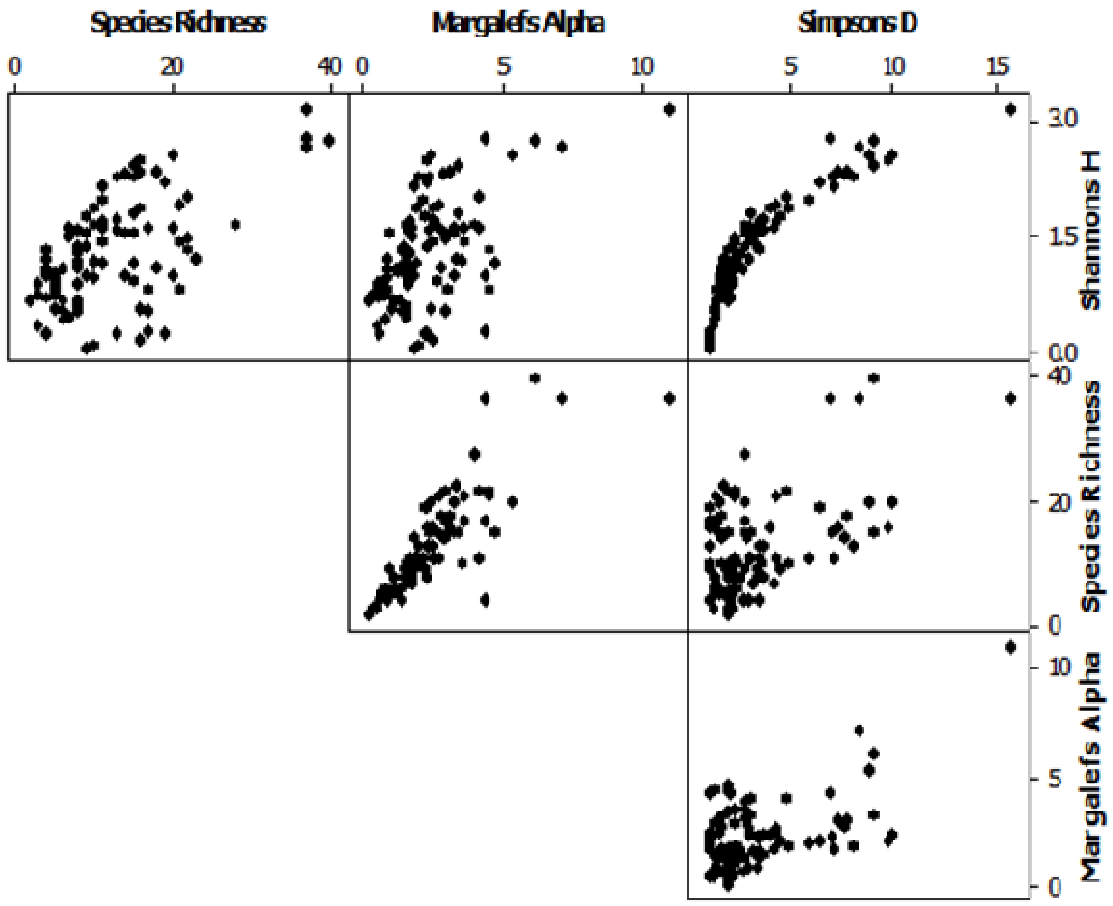

Figure 4.4. Matrix plot of species diversity indices for the Nansen West Coast survey.

The contour maps of the four species diversity indices for the Africana South Coast samples (Figure 4.5) revealed relatively low species diversities across most of the north and south-eastern areas, with the higher diversities generally located in the south-western area. One conspicuous zone of higher species diversity was located south of latitude 36°, between longitude 20°E and 22°E, indicated by the dark green coloured pocket in the lower left hand corners in all four plots. The contour plots for the Africana West Coast samples (Figure 4.6) revealed that the species diversity of the benthic epifauna was distributed heterogeneously. Most of the samples supported relatively low species diversities, but zones of higher species diversity were dispersed throughout the south-western region of the sampling area, generally in deeper water, below the level of the continental shelf. One conspicuous zone of higher species diversity was located south of latitude 31.5°S, between longitude 16°E and 17°E, indicated by the darker coloured area near the centre in all four of the plots.

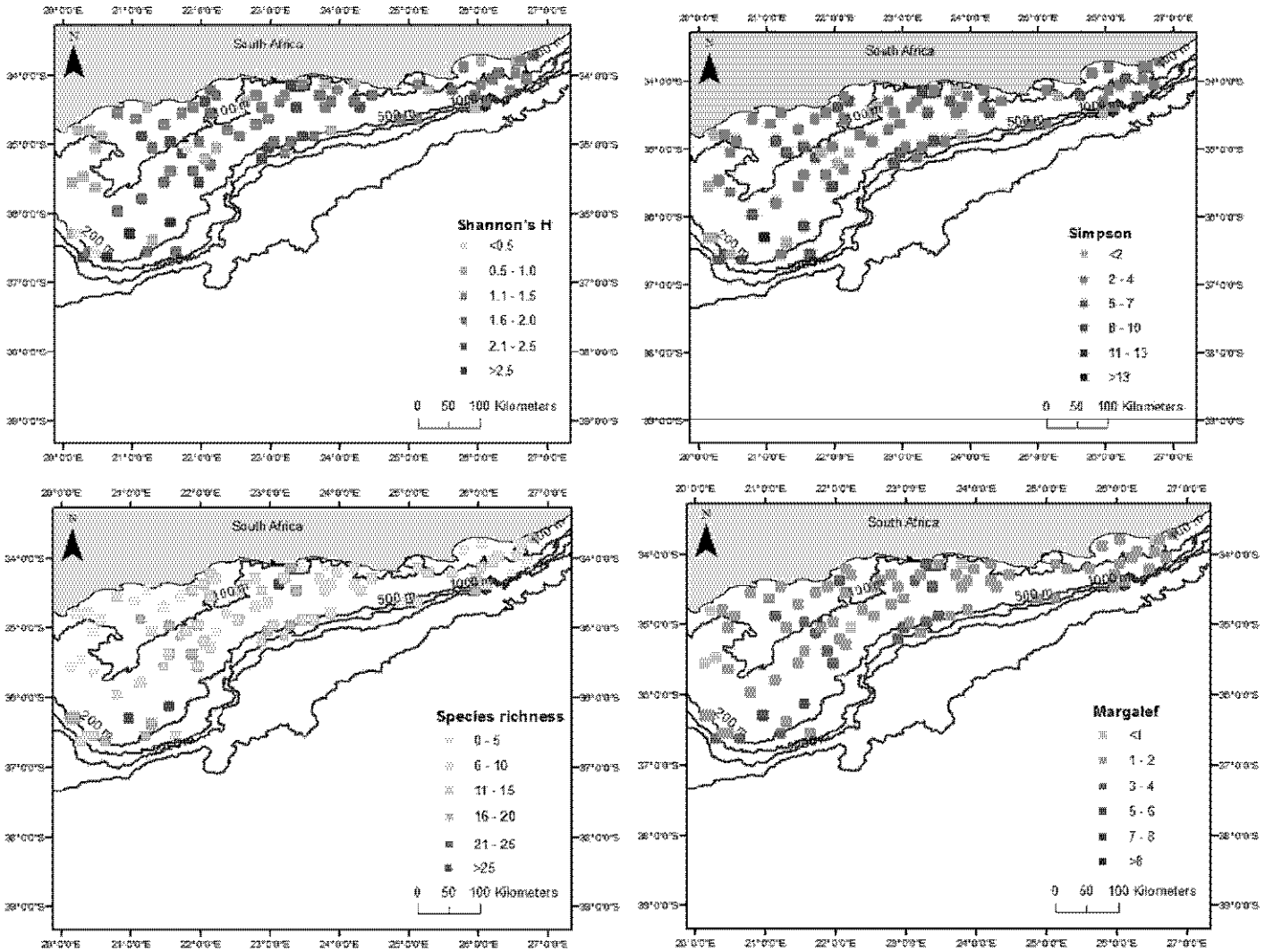

Figure 4.5. Bathymetric maps of species diversity indices for the Africana South Coast survey.

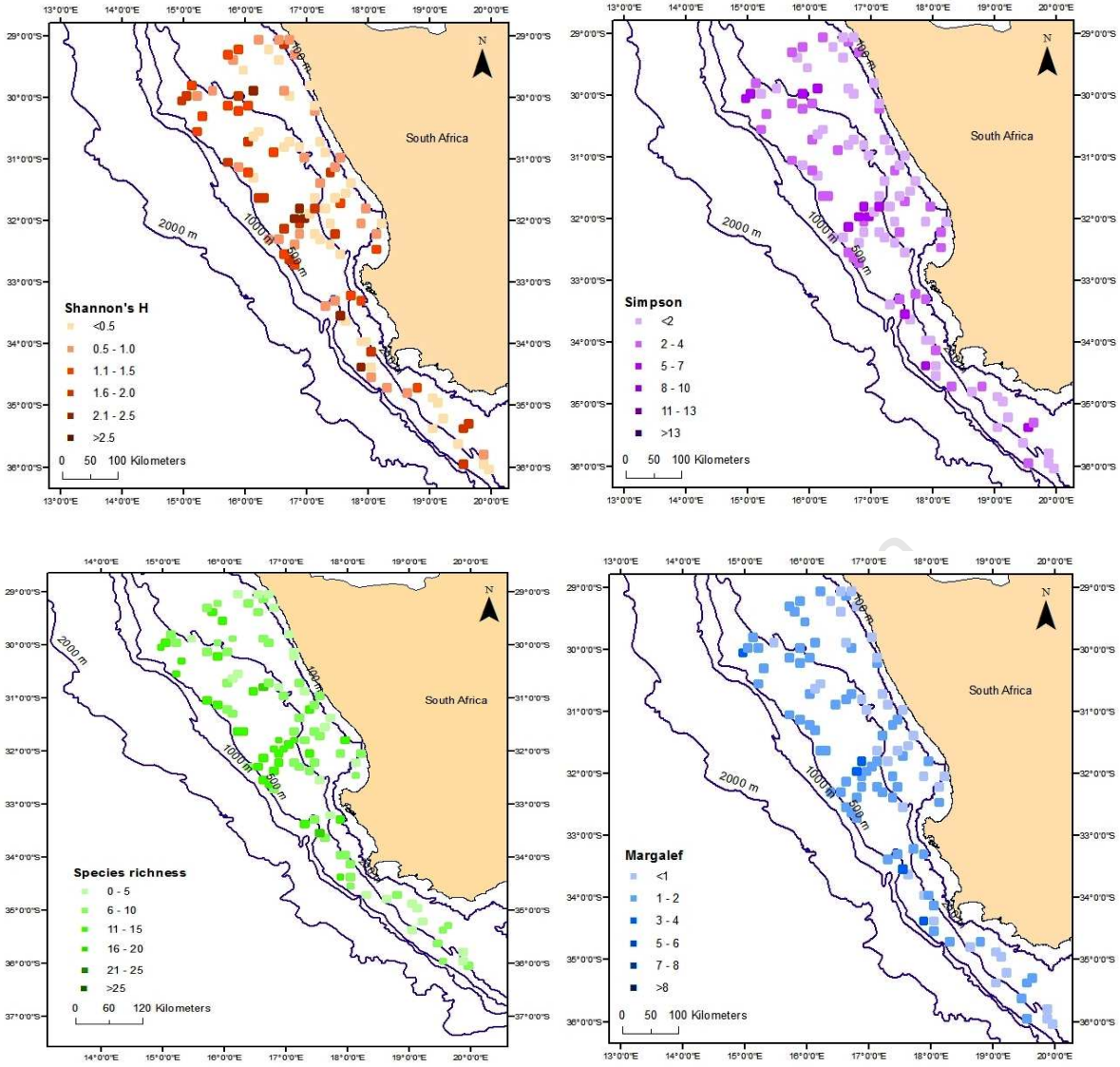

Figure 4.6.Bathymetric maps of species diversity indices for the Africana West Coast survey.

The contour maps of the four species diversity indices computed from the samples collected during the Nansen West Coast survey (Figure 4.7) revealed one conspicuous zone of higher species diversity located around latitude 31.5°S, between longitude 16.35°E and 16.67°E. This zone is indicated by the darker green coloured areas near the top left hand corner in all four of the plots. The same zone of high species diversity is also conspicuous (dark green areas) on the contour plots produced from the samples collected during the Africana West Coast survey (see Figure 4.6 for comparison).

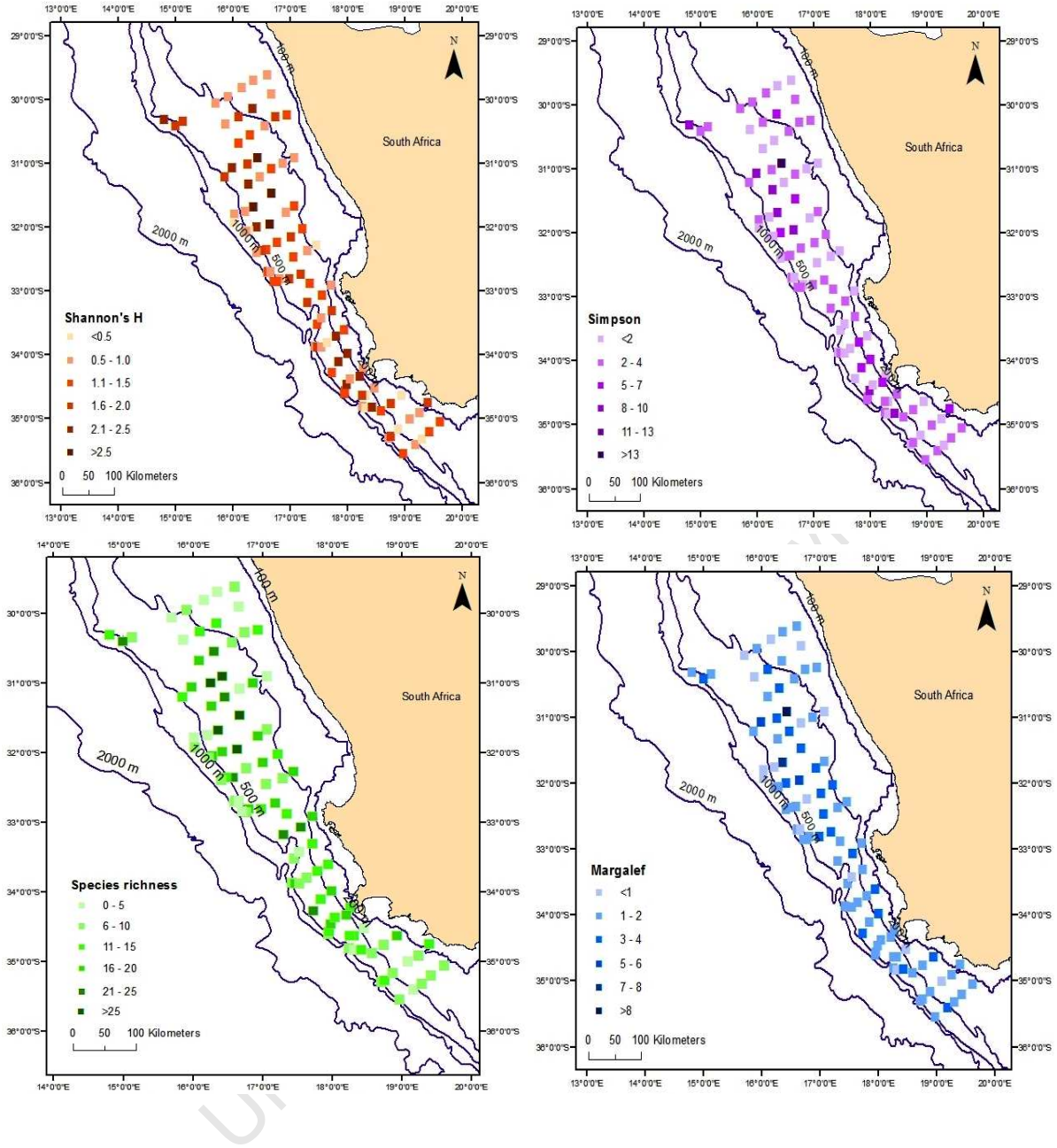

Figure 4.7. Bathymetric maps of species diversity indices for the Nansen West Coast survey.

4.3.3. Relationships between species diversity and environmental variables for the Africana and Nansen surveys

These analyses were based on the groups/communities that were determined in the previous two chapters by hierarchical cluster analyses. It was not possible to perform an ANOVA to compare the mean species diversity indices and the mean values of the physico-chemical variables across the groups of sampling sites clustered by similar species compositions for the same reasons as provided in Chapter 2, section 2.5.8.

Box plots were constructed to visualize any systematic relationships between the groups/communities (determined by the cluster analyses in Chapter 2 for the Nansen survey, and in Chapter 3 for the Africana survey) and the species diversity indices. The box plots represent the species diversity indices partitioned into quartiles, and the centre lines represented the medians (Figure 4.8). The lowest species diversities were consistently in groups 4 and 10, while the highest were consistently in group 13 (Figure 4.8).

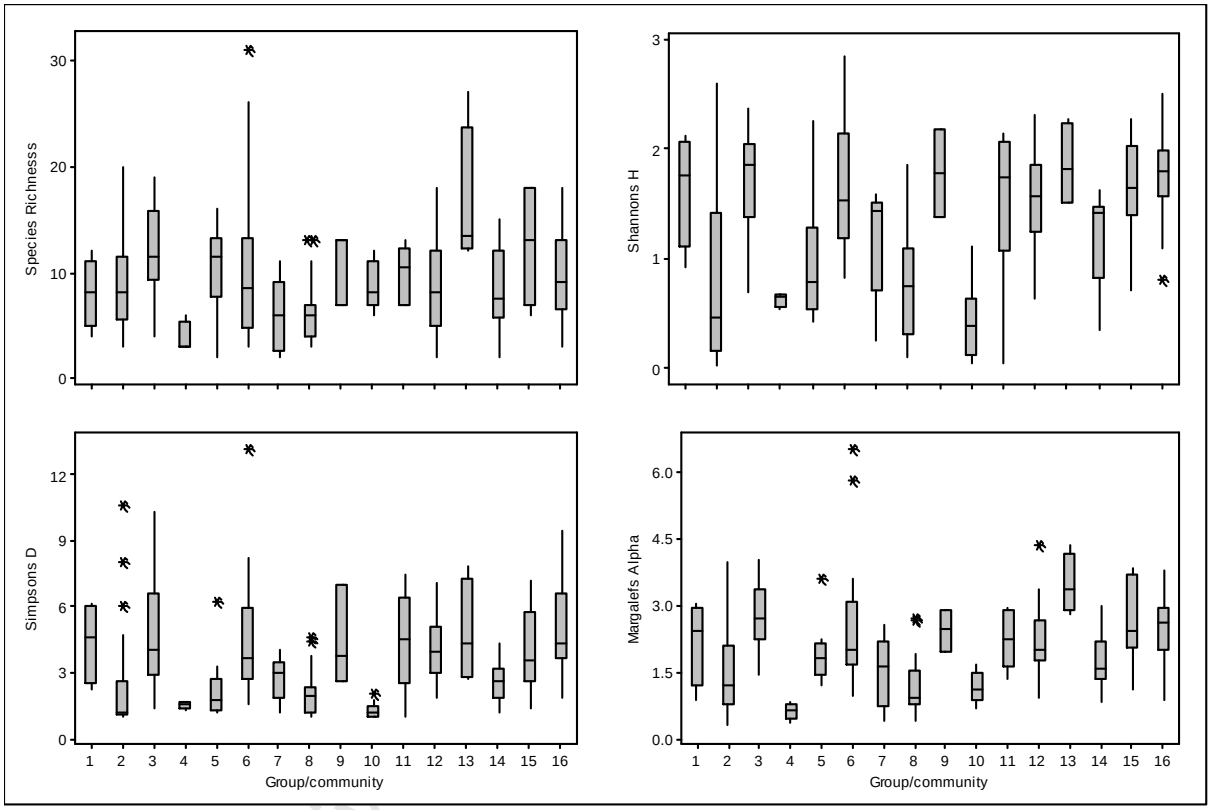

Figure 4.8. Relationships between the five site groups and species diversity for the Africana South Coast survey (* denote outliers).

Sites in group 6 were located south of latitude 36^{o} between longitude 20^{o}E and 22^{o}E. These sites were reflected by the conspicuous deep coloured sites in Figure 4.5. Sites in group 2, located further north at latitude 34^{o} 59'S, was also observed as darker sites in Figure 4.5. Group 13 had the highest species diversity and was characterised by having sand or muddy-sand substrates, occurring between 450 - 500 m depth intervals, with low temperatures of approximately 7℃. Group 4 displayed the lowest species richness, while group 10 was identified with the lowest Shannon's H, Simpson's D and Margalef's Alpha values. This group was observed in shallow waters in depths of <150 m, with low dissolved oxygen (DO) of <2 ml/L.

Box plots indicated that species richness, Shannon's H, Simpson's D and Margalef's Alpha for the samples collected during the Nansen West Coast survey did not vary systematically between the

groups/communities extracted by cluster analysis in Chapter 2 (Figure 4.9). Groups 1 and 2 contained numerous outliers (denoted by *) representing sites with unusually high levels of species diversity. It was evident that the classification and ordination methods used to analyse the data collected from the Nansen survey did not identify distinct groups of sites with high species diversity.

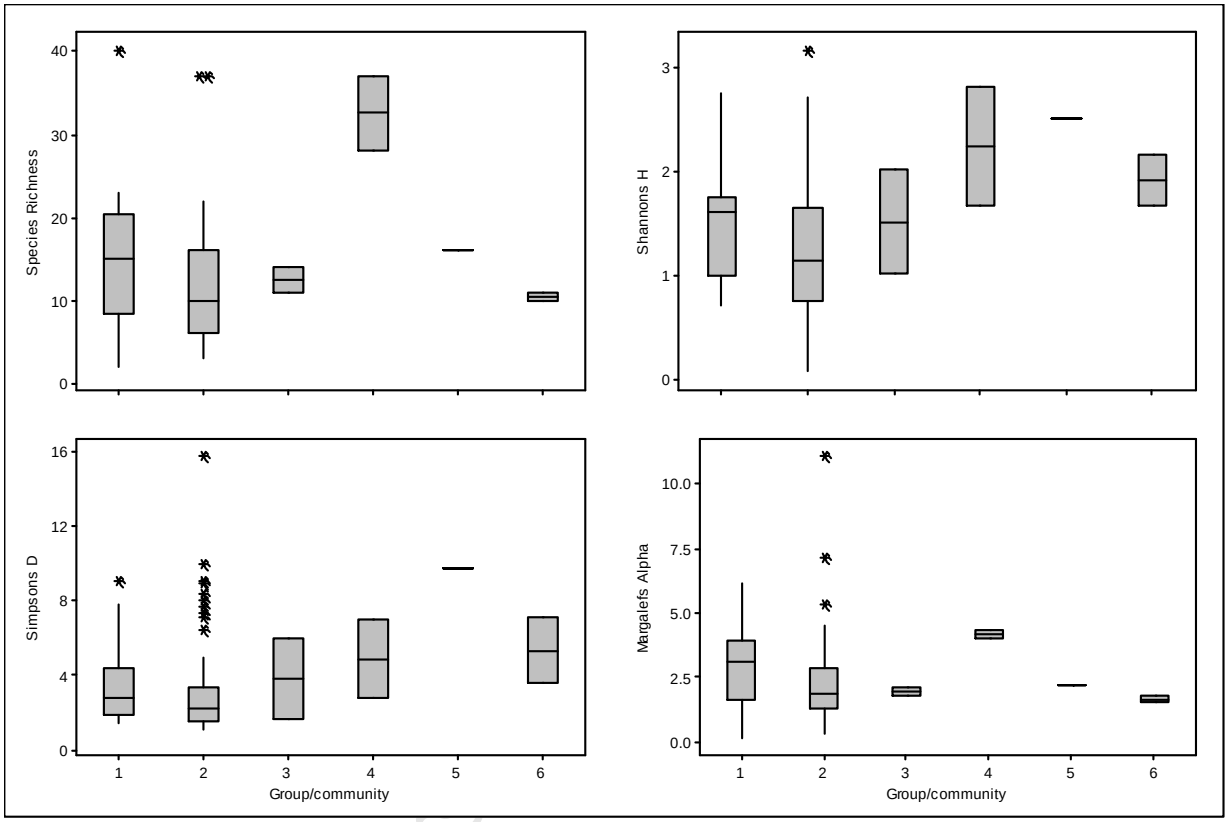

Figure 4.9. Relationships between the six site groups and species diversity for the Nansen West Coast survey (* denotes outliers).

4.3.4. Multiple linear regression analysis for the Africana surveys

Multiple linear regression analysis was performed using the combined data from the Africana South Coast and West Coast surveys (hereafter referred to as the Africana survey). The values in all the tables below with * next to them should be considered significant.

Table 4.2. Correlation matrix for the Africana survey conducted offshore of the South and West Coasts of South Africa.

	logt Species Richness	Shannon's H	Logt Simpson's D	Margalef's Alpha	Logt Depth	DO Squared	Logt Salinity
Shannon's H	0.480*						
Logt Simpson's D	0.349*	0.975*					
Margalef's Alpha	0.753*	0.823*	0.823*				
Logt Depth	0.305*	-0.028	-0.028	0.083			
DO Squared	0.244	0.312*	0.278*	0.370*	0.157*		
Logt Salinity	-0.164*	-0.159*	-0.173*	0.064	-0.841*	0.087	
Logt Temperature	-0.174*	0.075	0.095	-0.001	-0.830*	-0.053	0.955*

* Significant at $p < 0.05$

For the Africana survey, species richness and the species diversity indices were positively correlated with each other at $p < 0.05$ (Table 4.2). Logt species richness was positively correlated with depth and negatively correlated with salinity and temperature at $p < 0.05$. Shannon's H and Logt Simpson's D were positively correlated with DO Squared and negatively correlated with Logt Salinity at $p < 0.05$. Margalef's Alpha was positively correlated with DO Squared at $p < 0.05$. There were significant correlations between Logt Depth, DO Squared and Logt Salinity, which indicated collinearity between the environmental variables.

Table 4.3. Correlation matrix for the Nansen survey conducted offshore of the West Coast of South Africa.

	Logt Species Richness	Shannon's H	Logt Simpson's D	Margalef's Alpha	Logt Depth	DO Squared	Logt Salinity
Shannon's H	0.547*						
Logt Simpson's D	0.772*	0.545*					
Margalef's Alpha	0.407*	0.969*	0.443*				
Logt Depth	-0.065	-0.016	-0.028	-0.059			
DO Squared	0.004	0.002	-0.006	-0.011	0.727*		
Logt Salinity	-0.053	-0.057	0.073	0.129	-0.867*	-0.662*	
Logt Temperature	0.104	0.115	0.122	-0.167	-0.857*	-0.712*	0.976*

* Significant at $p < 0.05$

For the Nansen survey, species richness and the species diversity indices were positively correlated with each other at $p < 0.05$, but not with any of the environmental variables (Table 4.3). There were significant correlations among Logt Depth, DO Squared and Logt Salinity, reflecting collinearity among the environmental variables.

Logt species richness was initially predicted using eight environmental variables (Table 4.4); however, the statistical inferences based on the t tests for the significance of the regression coefficients were compromised by collinearity between salinity and temperature, and between sand and sand and mud, indicated by VIF > 5.

Table 4.4. Prediction of Logt species richness using eight predictor variables for the Africana survey conducted offshore of the South and West Coasts of South Africa.

Predictor	β Coefficient	SE	t	p	VIF
Intercept	142.88	6.08	2.38	0.019*	
Coast	0.298	0.059	5.01	<0.001*	3.447
Logt Depth	0.471	0.136	3.47	0.001	4.556
DO2	-0.004	0.007	-0.52	0.604	2.235
Logt Salinity	-94.09	39.40	-2.39	0.018*	21.950
Logt Temperature	1.939	0.823	2.35	0.020*	15.828
Sand	-0.036	0.091	-0.40	0.691	8.157
Sand and Mud	-0.107	0.094	-0.11	0.909	8.316
Mud	-0.130	0.142	-0.93	0.360	1.751
D-W	1.386*				
Critical D-W	1.670				
Adjusted R2	21.5%				

* Significant at $p < 0.05$

New predictor variables were constructed by addition of the collinear variables, specifically Logt Salinity + Logt Temperature, and Sand + Sand and Mud (Table 4.5). Collinearity was eliminated indicated by VIF < 5. In the absence of collinearity, using six predictor variables, Coast and Logt Depth were significant predictors of Logt species richness at $p < 0.05$.

Table 4.5. Prediction of Logt species richness for the Africana survey conducted offshore of the South and West Coasts of South Africa, using six predictor variables.

Predictor	β Coefficient	SE	t	p	VIF
Intercept	-0.792	1.158	-0.68	0.495	
Coast	0.230	0.055	4.32	<0.001*	2.701
Logt Depth	0.558	0.128	4.35	<0.001*	3.972
DO2	-0.008	0.007	-1.16	0.248	2.072
Logt Salinity + Logt Temperature	0.179	0.382	-0.47	0.639	3.472
Sand + Sand and Mud	-0.023	0.092	-0.26	0.798	1.721
Mud	-0.142	0.143	-0.99	0.320	1.732
D-W	1.293*				
Critical D-W	1.682				
Adjusted R2	19.5%				

* Significant at $p < 0.05$

The inferences were that the sampling sites from the South Coast were, on average, predicted to have higher species richness than those from the West Coast, and that Logt species richness increased in proportion to Logt Depth. The R^2 value of 19.5%, however, reflected that the effect of the variance in Coast and Logt Depth on the variance in Logt species richness was relatively small. Autocorrelation was significant, indicated by the low D-W statistic which was less than the critical value. The cause appeared to be the cyclic patterns in Logt species richness across the time-series of sampling, which could not be eliminated. The implications of autocorrelation were that the predictive precision of the model was low, and that 95% confidence intervals could not be accurately computed to determine the precision of the predicted values.

The same method developed to predict Logt species richness was applied to predict Shannon's H (Table 4.6), Logt Simpson's D (Table 4.7) and Margalef's Alpha (Table 4.8).

Table 4.6. Prediction of Shannon's H for the Africana survey conducted offshore of the South and West Coasts of South Africa, using six predictor variables.

	β Coefficient	SE	t	p	VIF
Intercept	3.082	3.359	0.918	0.360	
Coast	0.776	0.155	5.020	<0.001*	2.701
Logt Depth	0.220	0.372	0.592	0.555	3.972
DO Squared	0.002	0.020	0.101	0.920	2.072
Logt Salinity + Logt Temperature	-1.237	1.107	-1.117	0.266	3.472
Sand + Sand and Mud	0.383	0.266	1.442	0.151	1.721
Mud	0.323	0.414	0.781	0.436	1.732
D-W	1.630*				
Critical D-W	1.682				
Adjusted R^2	20.9%				

* Significant at $p < 0.05$

Table 4.7. Prediction of Logt Simpson's D for the Africana survey conducted offshore of the South and West Coasts of South Africa, using six predictor variables.

	β Coefficient	SE	t	p	VIF
Intercept	1.648	1.386	1.19	0.236	
Coast	0.288	0.064	4.52	<0.001*	2.701
Logt Depth	-0.014	0.154	-0.09	0.928	3.972
DO Squared	0.002	0.008	0.19	0.852	2.072
Logt Salinity + Logt Temperature	-0.611	0.457	-1.34	0.183	3.472
Sand + Sand and Mud	0.190	0.110	1.73	0.086	1.721
Mud	0.192	0.171	1.12	0.262	1.732
D-W	1.693*				
Critical D-W	1.682				
Adjusted R2	18.3%				

* Significant at $p < 0.05$

Table 4.8. Prediction of Margalef's Alpha for the Africana survey conducted offshore of the South and West Coasts of South Africa, using six predictor variables.

	β Coefficient	SE	t	p	VIF
Intercept	-0.025	4.608	0.918	0.996	
Coast	1.298	0.212	5.020	<0.001*	2.701
Logt Depth	1.309	0.510	0.592	0.011*	3.972
DO Squared	-0.007	0.027	0.101	0.789	2.072
Logt Salinity + Logt Temperature	-0.742	1.519	-1.117	0.626	3.472
Sand + Sand and Mud	0.427	0.364	1.442	0.243	1.721
Mud	0.055	0.568	0.781	0.923	1.732
D-W	1.408*				
Critical D-W	1.682				
Adjusted R2	20.9%				

* Significant at $p < 0.05$

The significant predictor for all the species diversity indices at $p < 0.05$ was the geographical location of the sampling sites. The species diversity was consistently predicted to be higher on the South Coast than on the West Coast, while Logt species richness and Margalef's Alpha were predicted to increase with respect to depth. Figure 4.10 illustrates the relationships between the species diversity indices and depth stratified with respect to the two Africana survey locations. The upward sloping linear regression lines comparing the relationships between species diversity and depth for the South and West Coasts were almost parallel, indicating that the patterns of increase in diversity with respect to depth were generally similar for both regions.

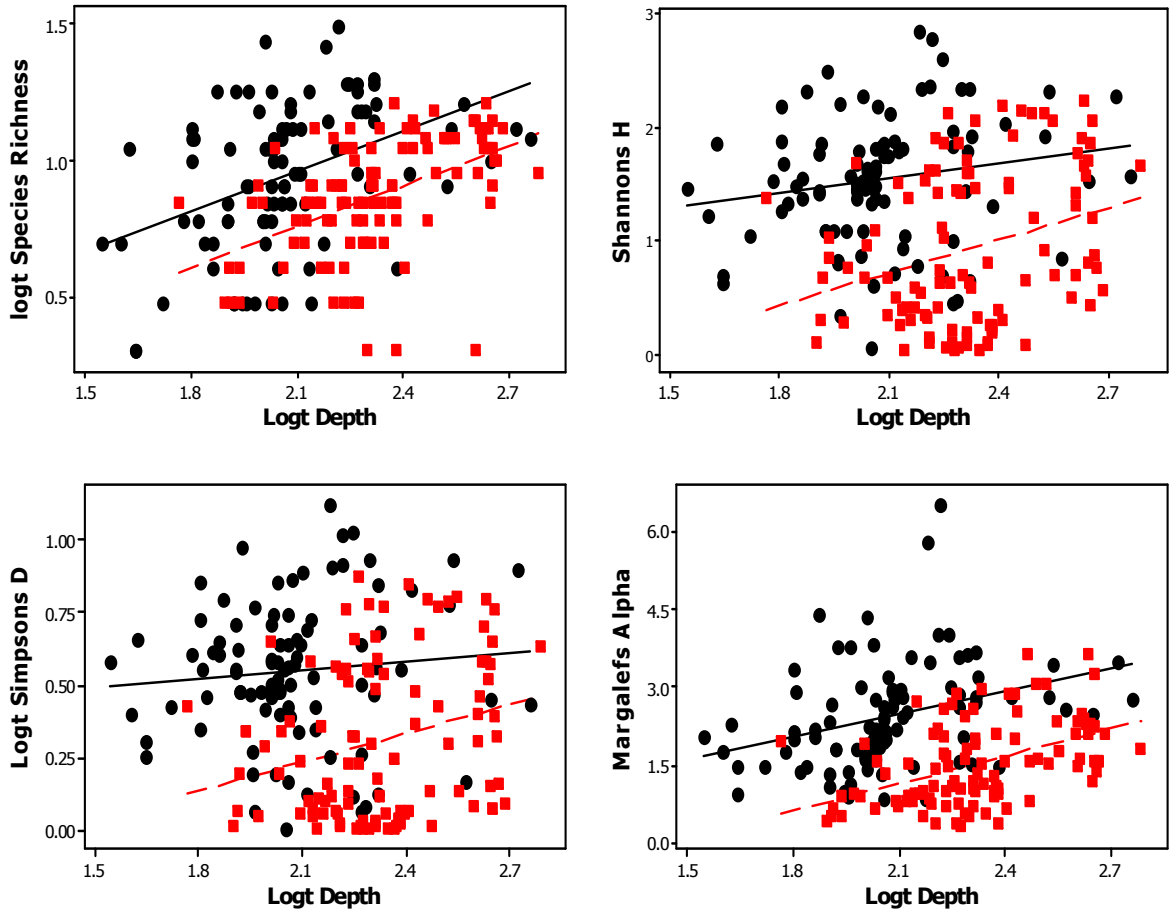

Figure 4.10. Relationships between the species diversity of the benthic epifauna and depth for the Africana South Coast and West Coast surveys.

Multiple linear regression analysis was performed for the Nansen survey to predict the species diversity indices from the environmental variables, using the same method described above for the Africana survey. Although co-linearity was eliminated, indicated by VIF < 5, no statistically significant regression models could be extracted from the data. None of the regression coefficients were significant at $p < 0.05$. For the Nansen survey, depth was not found to be a significant predictor of the species diversity of the benthic epifauna, as found in the Africana survey. The R^2 values were <3% and autocorrelation was significant. The non-significant regression statistics were used to predict Logt species richness in Table 4.9. The regression analysis to predict Shannon's H, Simpson's D and

Margalef's Alpha for the samples collected during the Nansen survey produced similar non-significant results at $p < 0.05$, and are not presented here as a result.

Table 4.9. Prediction of Logt species richness for the Nansen survey conducted offshore of the West Coast of South Africa.

Predictor	β Coefficient	SE	t	p	VIF
Intercept	-1.202	2.334	-0.51	0.608	
Logt Depth	0.003	0.284	-0.01	0.992	4.249
DO2	0.006	0.009	0.68	0.496	2.349
Logt Salinity + Logt Temperature	0.710	0.733	0.97	0.335	4.090
Sand + Sand and Mud	0.400	0.283	1.41	0.162	3.120
Mud	0.526	0.346	1.52	0.132	3.130
D-W	1.408*				
Critical D-W	1.682				
Adjusted R2	0.0%				

* Significant at $p < 0.05$

4.4. Discussion

As a preface to this discussion, it should be reiterated that this study was limited to sampling soft surficial sediments, which represent a very homogenous habitat low in biodiversity. Higher biodiversity can be expected to occur on hard heterogeneous substrata, as the more heterogeneous the habitat (the seafloor in this case), the higher the diversity (Gray, 2000). These soft sediment habitats also have a long history of commercial trawling (Lombard *et al.*, 2004), which may have reduced the abundance, or even species richness, of the biota over time. The effects of trawling on this habitat were not within the scope of this study, although comparison of these data with those from early historical trawls in the same region might form an interesting subject for later research. When the available historical data (collated in Chapter 1 and summarised below) are examined, the UCT Ecological dredge surveys conducted along the South and West Coasts of South Africa display very high species richness (971 species from dredge and grab samples, and 509 species from dredge and grab samples, respectively; Medd, 2007). The current survey results (Africana South Coast = 95 species, Africana West Coast = 63 species, and Nansen West Coast = 103 species) seem to indicate that species diversity is lower. However, it should be noted, as stated in Chapter 1, that the historical data were collected in much shallower depths close to the coast and that these species numbers consisted of fish, benthic and planktonic invertebrates, while the current study only collected larger offshore benthic invertebrates from depths >35 m. There is also a profound difference in gear as the UCT Ecological Survey dredges were lined with a 1 mm mesh liner, which retained much smaller and more species-rich taxa, such as amphipods and isopods, than were collected in the current study. As a result, the nearshore (historical data) and offshore (current study) data cannot be compared.

The species area curves for the West Coast of South Africa (Nansen and Africana surveys) appear to still be gradually rising (Figures 4.2b and 4.2c), indicating that this region requires further sampling to exhaustively determine the species that occur there. In contrast, the species area curve plotted for the South Coast has reached a plateau (Figure 4.2a), indicating that the area has been representatively

sampled throughout the present survey. The result of these findings suggests that future sampling is required offshore along the West Coast of South Africa in order to fully catalogue the benthic communities.

Despite the limitations described above, the Africana survey revealed a positive relationship between species number and increase in depth (Table 4.5). This is contrary to the findings observed for the Nansen West Coast survey, where no such relationship was apparent (Table 4.9). Additionally, along the West Coast of South Africa, the highest species numbers were found in the 0 - 99 m and 300 - 399 m depth intervals for both the Nansen and Africana surveys. It is important to note that along the continental shelves of the world's oceans the number of species and bathymetry shows a wide variety of relationships. For example, depending on the area studied, some authors have observed a positive relationship between species richness and depth (Weinberg, 1994; McClatchi *et al*., 1997; Labropoulou and Papaconstantinou, 2004), while others showed a negative relationship (Barber *et al.*, 1997; Fariña *et al.*, 1997; Sousa *et al.*, 2006), or no relationship at all (Mueter and Norcross, 1999; Colloca *et al.*, 2003), similar to the findings of the Nansen West Coast survey.

The findings of the current study, combined with those discussed above, reveal that using environmental variables (other than coast and depth) as predictors of species richness is not an appropriate method when searching for marine areas to protect. The current study found that species richness is higher offshore and to the south-west on the South Coast (Figure 4.5), and to the north-west along the West Coast (Figure 4.6), hence establishing a latitudinal difference in species richness. These findings are similar to those of Witman *et al. (*2004), which showed a latitudinal decrease in species richness in both the Northern and Southern hemispheres. Okuda *et al.* (2009), however, found that trends in species richness are not as clear on smaller scales. Latitudinal diversity of inshore marine taxa, measured as species richness for southern African species, has also shown increases in diversity towards the higher latitudes (Hockey and Branch, 1994; Scott, 2009), which were also observed in this study in the offshore South Coast region (Figure 4.5). The increase in diversity with latitude clearly indicates that the South Coast supports a higher diversity of benthic epifauna per unit area than the West Coast. The differences observed between these two regions is likely due to the warming effect of the fast-flowing Agulhas Current that would enable the South Coast to support more tropical and warm-temperate species (Gyory, 2004).

These findings can be compared to those of the literature review conducted on the topic of a nearshore survey along the coast of South Africa by Awad *et al.* (2002). They found that species richness displayed strong peaks in areas of high sampling activity (False Bay, Port Elizabeth and Durban). Some taxonomic groups (gastropods, bivalves and echinoderms) displayed increased species richness from west to east, while for other groups (polychaetes and octocorals) the species richness was highest along the South Coast of South Africa (Awad *et al.*, 2002). The current offshore study displayed the same pattern, with species numbers increasing with latitude from west to east, with the South Coast having the highest species richness (Arthropoda, Asteroidea, Gastropoda and Porifera). It is important to note, however, that the current survey did not cover the full East Coast of

South Africa, as did the 2002 study. Interestingly, Scott (2009) found that the inshore species richness patterns of South Africa might be related to sea surface temperature, or life-history characteristics. The 2002 study collected 2 533 species (Awad *et al.*, 2002), which could be attributed to the shallow depth from which sampling was conducted, and the fact that the entire South African shoreline was sampled. Awad *et al.* (2002) also postulated that invertebrate distribution patterns along the South African coastline could be partially attributed to sampling bias and partially to changing environmental conditions. However, this is not comparable with the current study which used a standardised sampling grid. Environmental conditions in the deeper waters sampled here are also very different from those in the coastal zone.

The maps (Figure 4.11 below) display very patchy diversities, and there do not appear to be any large scale geographical patterns, as suggested by Lombard *et al.* (2004). There are more isolated patches of high diversity, possible representing small areas of different habitats, which could be due to environmental variables. This can only be confirmed with a fine scale offshore study of the areas of high diversity.

Soetaert and Heip (1990) concluded that the sample-size sensitivity of many diversity indices is a fundamental disadvantage, as this makes it difficult to compare among studies, however, some comparisons can be made. The Africana West Coast survey in this study displayed a similar pattern to that across a continental slope in the North Eastern Atlantic (Flach and De Bruin, 1999), where Shannon's diversity increased with water depth. A study along the continental shelf of the Gulf of Lions (Mérigot *et al.*, 2007) found similar patterns for the Shannon and Simpson diversity indices. A study conducted on the Brazilian South Eastern shelf also determined that species richness and the Shannon index did not generally vary significantly (De Léo and Pires-Vanin, 2006). Cleary *et al.* (2005) concluded, using Shannon's diversity index, that there was maximum diversity at an intermediate offshore distance and lower diversity near to the coast, again similar to the findings of the current study (Figure 4.11). It is thought that depauperate assemblages in nearshore environments are due to high pollution and eutrophication of the areas with fluvial discharge (Carballo *et al.*, 1996; Langer and Lipps, 2003; Du Châtelet *et al.*, 2004). The increase in diversity with depth has also been attributed to environmental stability at depth, the source-sink hypothesis, and effects of immigration, predation and energetic restrictions on the reproductive viability of macroinvertebrates (Rex *et al.*, 2005). In this present study the Shannon diversity index displayed an overall high diversity for the offshore region of South Africa, when compared to other regions, such as the deep sea of the Western Mediterranean (Cartes *et al.*, 2009) and the South Western Gulf of Mexico (Escobar-Briones *et al.*, 2008). The high local diversity was attributed in another study to sediment heterogeneity, since the composition of soft sediment benthic communities is linked to sediment characteristics (Etter and Grassle, 1992). It has also been suggested that biological disturbance by large organisms (Dayton and Hessler, 1972), geographic and temporal mosaics of patchiness resulting from organic enrichments (Grassle and Maciolek, 1992), and topographic variability focusing organic carbon deposits (Snelgrove and Smith, 2002), all contribute to high local diversity.

As the Shannon's diversity index can be used to assist in planning conservation areas it has been incorporated into the environmental legislation in certain countries, such as Norway (Molvaer, 1997). Areas of high diversity values that exhibit a higher Shannon's diversity index can be selected as important areas for protection, if biodiversity conservation is the aim of the managers of the protected areas. Diversity maps are a useful instrument for decision makers in delineating high diversity areas (Mercks *et al.*, 2009). Based on the findings from this current study, reliable maps of species richness and diversity have been created for the offshore region of South Africa (Figure 4.11). If these maps were to be placed together with fish species richness and diversity maps, as well as maps depicting meiofaunal diversity and richness, a comprehensive picture of important areas for conservation will begin to emerge.

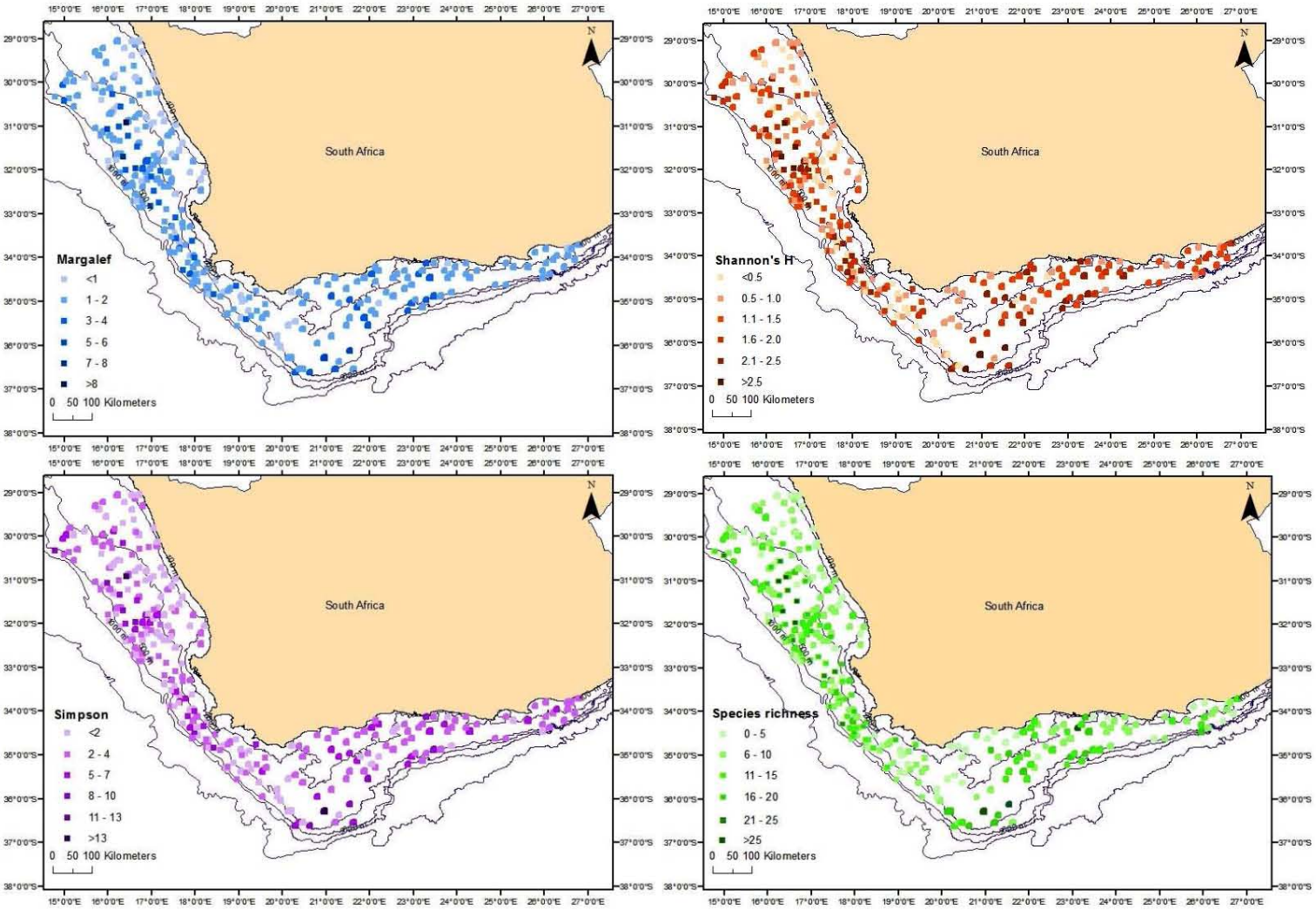

Figure 4.11. Maps displaying the four diversity indices (Margalef's Alpha, Shannon's H, Simpson's D and species richness) determined during the current study. The Africana West Coast, Africana South Coast and Nansen West Coast surveys have all been combined for this depiction.

Chapter 5

SYNTHESIS

"A dredging (in this case trawling) ship may be compared with an air-ship towing a dredge (or trawl) over Copenhagen, catching a policeman in one street and a perambulator in another: and from these it draws conclusions as to the whole population of the town" (Petersen, 1913). This quote expresses in layman's terms exactly how accurate the work of benthic ecologists is and this should be kept in mind at all times where the benthic environment is concerned. Research efforts aimed at mapping benthic environments, and understanding the relationships between seafloor environments and their associated benthic communities have increased in recent years (Zajac, 2008; and references therein). However, our knowledge of the offshore benthic environment of South Africa remains limited. As human impact on the oceans continues to increase, it is crucial to understand the patterns and changes in biodiversity, but without knowing what is in our oceans to begin with, the impacts that human activities have had, and continue to have, on these communities cannot be correctly established.

The aim of this study was to determine whether the benthic environment offshore of South Africa is made up of major regional zones, as suggested by Lombard *et al.* (2004), or whether the patterns of distribution within the benthic community or groups fail to adhere to these boundaries. Determining the patterns and determinants of soft-sediment biodiversity is vital to our overall understanding of marine processes. This study was the first to provide baseline information on the distribution patterns of benthic invertebrates communities at a large-scale offshore of South Africa. This information is key to the selection and management of offshore marine reserves in the region.

Chapter 1 documented the history and geographic scope of benthic invertebrate research in South Africa. Benthic samples were first collected in 1873 in South African waters, and sampling continued until the 1980's, over which time 2 504 benthic community-level samples were collected. These consisted of dredge, grab and trawl samples. Offshore sampling peaked in the 1890's and in the 1960's. Over this period of 107 years only 39 samples per 1000 km^2 were collected in depths of less than 100 m, and most of the data were non-quantitative, as various collection methods were used. These samples are also very unevenly distributed around the South African coastline, and are centred around major coastal cities (Griffiths *et al.,* 2010). The 100 - 200 m depth stratum also only makes up 10 % of the EEZ (Griffiths *et al.,* 2010). All other depth intervals, between 200 and 5700 m have less than five samples per 1000 km^2. It became apparent that the lack of sampling of the benthic environment in South Africa was a major concern. Following this period benthic invertebrates were only accidentally caught as bycatch during surveys for fish, implying that they were discarded afterwards. Hence, very few samples have been collected over the last 30 years.

Chapter 2 analysed the benthic invertebrate data collected during the *R/V Dr Fridtjof Nansen* cruise in 100 - 700 m water depths, along the West Coast of South Africa. In total 45 436 individual invertebrates were collected, representing 103 different species, grouped into 16 major taxonomic groups (Anthozoa, Asteroidea, Bivalvia, Demospongiae, Echinoidea, Gastropoda, Gymnolaemata, Hexactinellida, Holothuroidea, Hydrozoa, Malacostraca, Ophiuroidea, Polychaeta, Polyplacophora, Porifera and Rhynchonellata). In terms of species richness Crustacea (Malacostraca) and Echinodermata (Asteroidea) were the two most diverse groups and these same two groups had the highest abundance and biomass values. The shallow water anemone crab *Sympagurus dimorphus* and prawn species *Funchalia woodwadi* were the species with the highest abundances, while the sponge *Haliclonissa sacciformis* had the highest biomass value, together with the rock lobster *Palinurus gilchristi*. The species distribution pattern was not attributed to any of the measured environmental variables during the Nansen West Coast survey.

The cluster analysis produced six groups/communities, however, only two were large groupings, one (groups/communities) dominated by the crab *Mursia cristiata*, and the second groups/communities (groups/communities 2), dominated by the shallow water anemone crab *Sympagurus dimorphus*. The remaining three groups/communities were isolated groups produced by the analysis made up of dominant species, but only comprising one or two samples. These groupings do not concur with the bioregions depicted in Lombard *et al.* (2004).

In Chapter 3 benthic invertebrate data collected aboard the research vessel the *F.R.S. Africana*, were analysed. In total 64 829 individual invertebrates were sampled along the South and West Coasts of South Africa. The South Coast was more species rich (95), and more unique species were found in that region, than on the West Coast (67).

On both the South Coast and the West Coast the Crustacea and Echinodermata were the two groups with the highest contributions to the biomass. The most important contributors to biomass on the South Coast were the shallow water anemone crab *Sympagurus dimorphus* and gastropod mollusc *Pleurobranchaea bubala*, while on the West Coast it was the rock lobster *Jasus lalandii* and once again the shallow water anemone crab *Sympagurus dimorphus.*

Along the South Coast Crustacea (Malacostraca) and Echinodermata species dominated the shallower regions (0 - 99 and 100 - 199 m), Crustacea (Malacostraca), Gastropoda and Asteroidea the mid-depths (200 - 499 m) and Crustacea (Malacostraca) and Asteroidea the deep areas (500 - 599 m). The highest biomass values recorded along the West Coast were for Crustacea (Malacostraca) and Asteroidea in the shallow depths (0 - 99 and 100 -199 m), and Crustacea (Malacostraca) in the deeper regions (300 - 699 m).

On the South Coast Gastropoda numerically dominated the 0 - 99 m depth interval and Crustacea had the highest abundance in all the remaining regions (100 - 599 m). On the West Coast Crustacea (Malacostraca) dominated the shallow depth intervals (0 - 399 m), Asteroidea the 400 - 499 m interval and Crustacea (Malacostraca) and Asteroidea the edge of the continental shelf (400 - 699 m).

Geographic location and depth were the major factors leading to the biogeographic patterning of the benthic invertebrates. Sixteen groups/communities were delimited during these two surveys, but once again six of these formed isolated groups (Group 1, 4, 9, 11, 13, 15) and two (group 6 and 7) spanned both the West and South coasts. The eight remaining groups/communities were distributed as follows: a continental slope group/community on the South Coast (group/community 3), occurring at the 500 m isobath, with its dominant species the deep water anemone crab *Parapaguris pilosimanus*; a small group (group/community 14), represented by the gastropod mollusc *Pleurobranchaea bubala,* and found to the east on the South Coast, stretching across depths; a third group/community (group/community 12) was also present on and around the 100 m isobath, dominated by the sea star *Astropecten irregularis*. The final large grouping located on the South Coast is group/community 16, represented b the crab *Mursia cristiata*. This group is present as a small, inshore group where this region of the coast is deeper inshore than at other points. Other groups along the West Coast included group/community 2, characterised by *Sympagurus dimorphus* and centred around the 200 m isobath; a large inshore group/community (group/community 8) represented by *Pterygosquilla armata*, and finally group/community 10, forming two small groups, one between 30°S and 29°S, and a seco nd grouping at 32°S, 17°E. This group was characterised by the sponge, *Suberites* sp. None of these groups/communities showed clear cut borders between them, and many of the groups/communities merge into one another or overlap their boundaries. As discussed in Chapter 3, these groups do not correspond to those regions proposed by Lombard *et al.* (2004).

The species that dominate each specific group/community can also be divided into a specific feeding guild, which can further assist the decision makers in planning MPA's (Table 5.1). Each group/community appears to have a specific feeding guild and this can give further insight into the same habitat at a finer scale. When one is aware of what type of feeding guild dominates an area, it is possible to recognize what type of species will most likely occur in that area and this could help decision makers when planning an MPA. For example, when an area has two main feeding guilds it will probably be more species diverse (although not more species rich) than another area where only one major feeding guild is dominant and if it is the decision maker's plan to conserve biodiversity, an area with more feeding guilds is preferable to an area with only one main feeding guild.

Table 5.1. Composite feeding guilds of groups/communities detected by the Nansen West Coast and Africana South and West Coast surveys.

Dominant Species	Group/Community	Feeding Guild
Mursia cristiata	Nansen group 1	Detritus feeder/predator/scavenger
Sympagurus dimorphus	Nansen group 2	Deposit feeder
Haliclonissa sacciformis	Nansen group 3	Suspension feeder
Balanophyllia sp.	Nansen group 4	Predator
Asteroidea sp. 20	Nansen group 5	Predator
Ophiuroidea sp. 500	Nansen group 6	Detritus/deposit/susupension feeder
Toraster tuberculatus	Africana group 1	Predator
Sympagurus dimorphus	Africana group 2	Deposit feeder
Parapaguris pilosimanus	Africana group 3	Deposit feeder
Jasus lalandii	Africana group 4	Predator
Solasteridae	Africana group 5	Predator/scavenger
Polychaeta sp. 6/ Holothuroidea sp. 4	Africana group 6	Deposit/detritus feeder/predator Browsing/grasing
Spatangus capensis	Africana group 7	Scavenger
Pterygosquilla armata	Africana group 8	Detritus feeder/predator/scavenger
Asteroidea sp. 36	Africana group 9	Predator
Suberites sp.	Africana group 10	Suspension feeder
Brisaster capensis sp.	Africana group 11	Deposit feeder
Astropecten irregularis	Africana group 12	Predator/scavenger
Rochinia hertwigi/ Echinus gilchristi	Africana group 13	Scavenger/detritus feeder Scavenger
Pleurobranchaea bubala	Africana group 14	Carnivore
Echinus gilchristi	Africana group 15	Scavenger
Mursia cristiata	Africana group 16	Detritus feeder/predator/scavenger

In Chapter 4 the various diversity and species richness indices were applied to the data collected on the South and West Coasts of South Africa. On the Africana South and West Coasts, the species richness increased with increasing depth, and decreased with increasing salinity and temperature. The species richness was also shown to increase from West to East. This is possibly due to the difference in bottom temperature of the two currents flowing through these regions- the warm Agulhas Current on the South Coast, and the cold Benguela Current on the West Coast (Roberts and Sauer, 1994).

According to the Shannon diversity index, South Africa's offshore regions displayed a high diversity compared to other studies (Flach and De Bruin, 1999). These types of indices become important when decision makers need to decide on areas most appropriate for conservation. The indices on their own

would not be appropriate to use as a tool for decision makers to delimit MPA's, as conservation decision makers are reluctant to make decisions based exclusively on biodiversity indices - they want more information based on single species. However, the indices would be a good tool to enhance the choices made by the managers and decision makers regarding MPA's.

The aim of this thesis was to determine if different groups/communities exist on the seafloor, and even though the data sets (Chapter 2 and 3) were separated due to their different sampling methods, the Africana West Coast and Nansen West Coast datasets displayed groups/communities with the same dominant species (Figure 5.1). The Africana dataset's group/community 2 corresponds to the Nansen dataset's group/community 2, both characterized by the shallow water anemone crab, *Sympagurus dimorphus*. Both group/community 1 of the Nansen data and group/community 16 of the Africana data had the crab species, *Mursia cristiata* as their major contributor. All these matching groups/communities are also found in the same region (Figure 5.2). This indicates that benthic invertebrates can successfully be used to delimit groups/communities across the ocean floor using the computer programme MINITAB 16.1 and GIS. However, the communities identified are dependent on assumptions made in the MINITAB 16.1 program and appropriate cut-off levels.

Figure 5.1 displays the great heterogeneity of the area sampled. Further sampling is highly likely to reveal that these communities are structured by a combination of both biology (dispersal) and their response to the environment (depth, temperature, oxygen and current speed).

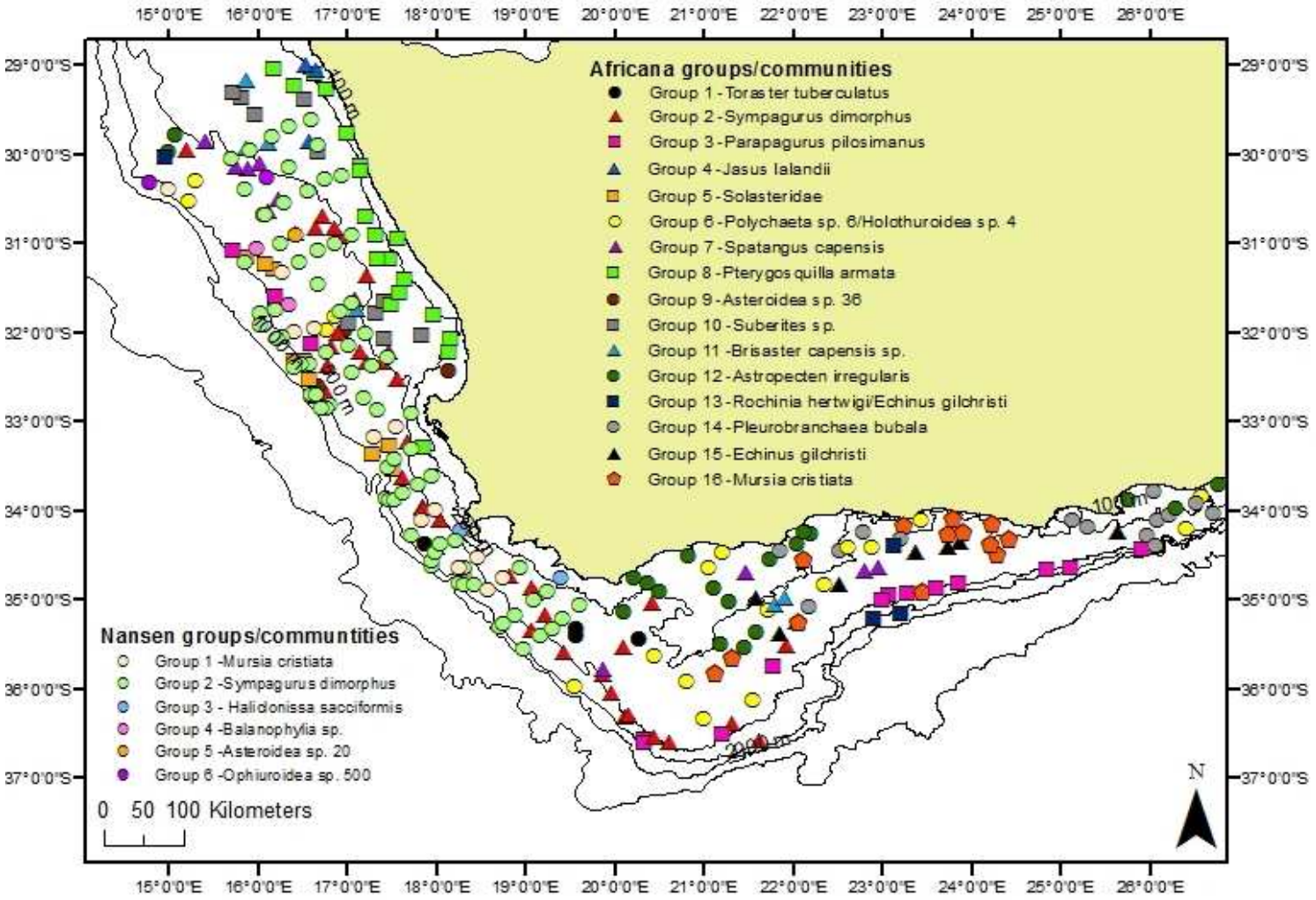

Figure 5.1. Composite map of groups/communities detected by the Nansen West Coast and Africana South and West Coast surveys.

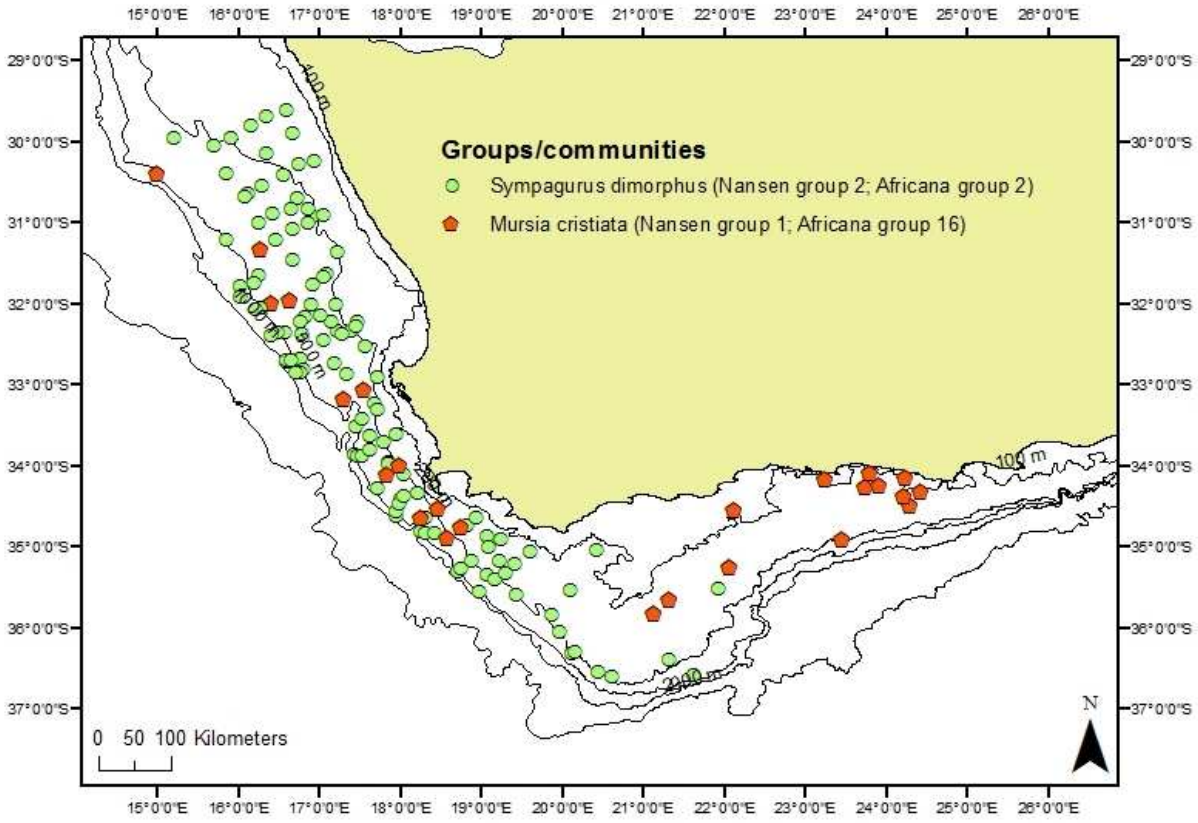

Figure 5.2. The Africana West Coast and Nansen West Coast datasets displayed groups/communities with the same dominant species.

Even though the groups/communities did overlap, statistical analyses were performed to compare the biomass and abundance values of the two West Coast surveys, by taxonomic groups. Results of the nonparametric Mann-Whitney U test (Table 5.2) revealed that the biomass for each taxonomic group (except for Polychaeta) was significantly different ($p < 0.05$) between the two cruises, and the same was shown for the abundance data (Ascidiacea and Bryozoa were not tested due to insufficient sample numbers being collected). Crustacea, Cnidaria, Echinodermata, Mollusca and Porifera were all significantly different in biomass and abundance between the two West Coast surveys (Table 5.2). Results from samples taken on the Nansen survey showed higher average abundance and biomass values (except the biomass of Porifera) than samples taken from the Africana West Coast survey. These significant differences are probably due to the different sampling techniques used. These included the random sampling design on the Africana West Coast cruise, versus the depth-stratified sampling technique on the Nansen West Coast cruise, and also different type of trawling nets employed on the two cruises, and their differing mesh sizes. However, it should be noted that the community structure at the level of major taxa was similar between the two cruises.

The above results imply that, if time and funding allows, it would be best and simpler to sample using a standardised method, i.e. only use a single type of gear and sampling technique when analysing entire community composition, so as to make the results comparable and hence the analyses and interpretation more robust.

Table 5.2. A comparison of the average abundance and biomass of major taxa recorded along the West Coast during the two different sampling cruises (Nansen West Coast Cruise and Africana West Coast Cruise).

	Average Abundance (ind/ha)		Average Biomass (g/ha)	
Taxonomic group	Nansen survey	Africana West Coast survey	Nansen survey	Africana West Coast survey
Bryozoa	2.54	0.43	4.23	1.16
Cnidaria	76.42	42.26	1828.26	254.14
Crustacea	466.62	131.00	7563.66	602.49
Echinodermata	101.84	3.09	1735.10	39.42
Mollusca	36.36	1.51	8711.83	56.86
Polychaeta	71.72	13.23	582.75	19.60
Porifera	538.34	144.23	8146.41	622.09

Comparing all three cruises (Nansen West Coast, Africana West Coast and Africana South Coast surveys) using the nonparametric Kruskall-Wallis statistical test showed that all taxonomic groups were significantly different ($p < 0.05$) in both abundance and biomass (Table 5.3). The differences on the West Coast are most likely due to the different sampling methods, while the South Coast is different due to the warm Agulhas Current flowing along the coast and the cold Benguela Current along the West Coast.

Table 5.3. A nonparameteric Kruskall-Wallis test showing the significant differences between the taxonomic groups during all three cruises.

Taxonomic group	Abundance (ind/ha)		Biomass (g/ha)	
	Kruskal-Wallis value	p-value	Kruskal-Wallis value	p-value
Cnidaria	K = 6.775	0.034	K = 8.071	0.018
Crustacea	K = 15.624	<0.0001	K = 7.757	0.021
Echinodermata	K = 6.968	0.031	K = 23.223	<0.0001
Mollusca	K = 18.412	<0.0001	K = 21.330	<0.0001
Porifera	K = 9.281	0.001	K = 6.47	0.016
Groups combined	K = 50.427	<0.0001	K = 68.098	0.0001

Table 5.4 lists previous studies undertaken along the South African coast that have attempted to distinguish groups/communities. However, most of these examined coastal or shallow subtidal systems (Bustamante, 1994; Bustamante and Branch, 1996; Christie, 1976; Emanuel *et al.,* 1992; Gumede, 2001; Lombard *et al.,* 2004; Olbers *et al.,* 2009; Sink *et al.,* 2005), and not offshore. Only Field (1971) and Christie (1976) delimited groups/communities from data collected via grab and dredge samples. It should be noted that all these studies in Table 5.4 have varying similarity levels, and therefore comparisons with the current study were not possible. Field found six distinct shallow water groups/communities (using a modified Van Veen grab to sample) in depths of 2 - 8 , 16 - 23 , 38, 58, 80 and 100 m along a transect in False Bay, South Africa. However, the current study had it shallowest trawl at 40 m depth, and the analysis did not define any specific shallow water groups/communities, as the trawls could not be conducted much shallower than this depth. Diving surveys might then provide a better idea of what the invertebrate biogeography patterns are in waters shallower than this. Since Field (1971) found several distinct zones, it is more than likely that there will be groups/communities in these shallow coastal regions - this is supported by the fact that Gumede (2001) delimited three groups/communities along the East Coast. Christie (1976) found three distinct bioregions between 0 - 33 m depth on the West Coast, the zones were characterised by depth, the first zone occurring at 0 - 1 m depth, the second at 3 - 5 m depth and the third at 10 - 33 m depth. These were slightly different from the Field (1971) study, however, this study was conducted along a transect in Lamberts Bay, on the West Coast, while the Field (1971) study was undertaken in False Bay. It is likely that the slight difference in groups/communities might be due to bottom water temperature, as Lamberts Bay is colder than False Bay, as well as the different sampling methods used in each study. Lombard *et al.* (2004) is the only other study where offshore groups/communities have been selected. However, they displayed six regions, along the entire offshore coast of South Africa where the current study was conducted (the Agulhas bioregion, the Atlantic offshore bioregion, Indo-Pacific offshore bioregion, Namaqua bioregion, South-west Indian offshore bioregion and the South-western Cape bioregion) based on depth (Chapter 3, Figure 3.9), while the current study found five groups/communities on the West coast during the Africana survey and six groups during the Nansen survey. The Africana dataset also produced three groups/communities along the South Coast and a further eight groups were found to span both the South and the West coast. The East Coast region was not included in this analysis and still needs to be assessed, but is sure to incorporate additional offshore bioregions.

Table 5.4. Groups/communities (faunistic groups) found by other studies undertaken in South Africa

Region	Depth (m)	Groups/ communities	Author
Aliwal Shoal, East Coast	10 - 24	3 (hard substratum)	Olbers et al., 2009
Lamberts Bay, West Coast	0 - 33	3 (soft substratum)	Christie, 1976
East Coast	25 - 45	4 (hard substratum)	Gumede, 2001
False Bay, South Coast	2 - 100	6 (soft sediment)	Field, 1971
Entire South African coast	Intertidal zone 0 - 10	3 (hard and soft substratum)	Bustamante, 1994
Entire South African coast	Intertidal zone 0 - 10	4 (hard and soft substratum)	Emanuel et al., 1992
KwaZulu-Natal, East coast	Intertidal zone 0 - 10	5 (hard substratum)	Sink et al., 2005
Entire South African coast	Intertidal zone 0 - 10	3 (hard and soft substratum)	Bustamante and Branch, 1996
Entire South African coast	0 - 500	8 (hard and soft substratum)	Lombard et al., 2004
Greater St. Lucia Wetland Park, East Coast	Coral reef ~20	6 (hard substratum)	Schleyer and Celliers, 2005

As mentioned in previous chapters, only soft sediment habitat was sampled during this study, due to the fact that trawling nets would tear if rocky or hard substrata were to be sampled. The total of 20 groups/communities that were recognised above thus only represents those groups/communities found on trawlable grounds or soft sediment within the depth range sampled. As the sampling region for this study is the site of commercial trawling, it should be noted that trawling can change/destroy the physical environment and the act of trawling can also completely remove species from the environment, thereby reducing species richness.

It is well known that in the coastal areas when sandy beaches are compared to rocky shores, the sandy beaches show much less diversity. According to Gray (1997) marine biodiversity is higher in benthic rather than pelagic systems, and in coasts rather than the open ocean, since there is a greater range of habitats near coasts. This was first noted by Simpson (1964), who stated that the more complex the physical environment, such as rocks, the more diverse the fauna. Coastal regions display a wide variety of habitats, such as sea grass beds, coastal sedimentary habitats, rocky shores, sandy beaches, kelp bed, mangrove forest, coral reefs and estuaries (Gray, 1997; and references therein), and it is for this reason that high diversity and consequently more groups/communities are found along the coastline. However, the offshore environment also exhibits various habitat types. Even though the current study only surveyed soft trawlable grounds, a plethora of environments still exists to be sampled. These include

the deeper continental edge, continental slope, untrawlable and hard grounds, sea mounts, abyssal plains, bathyal environments, submarine canyons, submarine carbon mounds, hydrothermal vents, trenches, cold water coral reefs and deep water reefs (Grassle, 1989, Sink *et al.,* 2010). Even within these environments further partitioning can occur as a result of biogeographic location, different sediment types etc. Coral reef environments are certainly not uniform and are also made up of reef flats, reef crests and reef slopes, all supporting different communities. Grassle and Maciolek (1992) noted that the enormous surface area of the deep ocean suggests that the number of species inhabiting the deep-seafloor has been greatly underestimated. It is thus probable that more groups/communities will become apparent as more sampling is conducted offshore in the various other habitats mentioned above, and these will in all likelihood be even more species rich than the soft sediment continental shelf.

It is expected that at least two additional soft substratum groups/communities will be found along the East Coast (KwaZulu-Natal), matching those found both on the West and South Coasts, but Schleyer and Celliers (2005) found seven distinct groups/communities when only assessing coral reefs found in KwaZulu-Natal at a 43 % similarity level (Table 3). Hence, it is likely that there will be more, as the depth gradient is stronger along this region and the continental shelf is very narrow compared to that on the West and South Coasts. Consequently, the steep continental slope is closer to the coast, implying that more groups/communities will be present, as there are a greater number of substrata (sediment types) and environments offshore of the East Coast (Dingle *et al.,* 1987; Sink *et al.,* 2010). In addition the warm Agulhas Current is much closer inshore along the East Coast, hence more tropical species should be present, which would mean different groups/communities. The current survey has shown that depth and geographic location are the major factors contributing to the distribution patterns of benthic invertebrates offshore of South Africa. However, since the depth stratum sampled was limited it is recommended that more measurements need to be collected at deeper depths across the EEZ in order to determine what effect these environmental factors have on the distribution patterns of deep sea invertebrates.

The South African EEZ extends to a depth of 5 700 m, of which only the 0 - 700 m component was surveyed in this study. This component of the EEZ covers 246 778 km^2 (Figure 5.3), leaving an enormous amount of the EEZ unsampled – that is the 82 849 360 ha that lies between 800 - 5 700 m depths. Much of this is too deep to sample, as South Africa does not have the equipment to sample to these depths, and the research trawls only reach depths of 700 m. Hence there are very few data available on the deep-sea (>700 m) benthic fauna of South Africa. It would be more viable to send a remote operated vehicle (ROV) down to the benthic environment to take photos and then interpret these. However, acquiring one of these and training someone to operate it will be costly.

It is not known what lies deeper than 700 m offshore of South Africa, as only the continental shelf has been surveyed. Other studies have shown that the deeper waters of the continental slope are even more

species rich than the continental shelf, however, the abyssal plains are less species rich, due to the constant environmental parameters found there (Rex, 1983; Paterson and Lambshead, 1995; Levin and Gage, 1998; Flach and De Bruin, 1999). Thus we can expect that further sampling along the continental slope and abyssal plains will yield more species, and hence more groups/communities at depths down to 5 700 m.

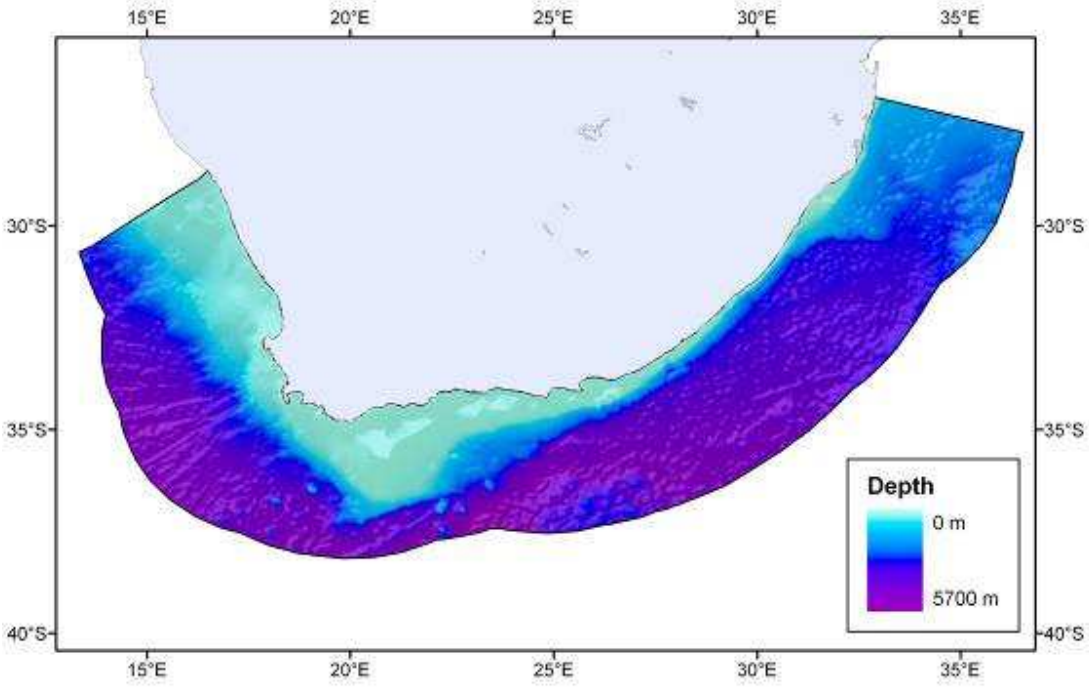

Figure 5.3. Map of the EEZ (Exclusive Economic Zone) of South Africa, indicating the depth in meters.

The East Coast, as previously stated, was excluded from this analysis and is sure to contain additional groups/communities, both because it represents a different biogeographical province and because substrate and sediment types in this region (Dingle *et al.,* 1987; Olbers *et al.,* 2009; Sink *et al.,* 2005) are more varied than on the South and West Coasts. Additional groups/communities will also surely be present on reef flats, reef crests and reef slopes, untrawlable grounds, deep reefs and hard grounds to name a few (Sink *et al.,* 2010). However, sampling this region is very difficult as there are few fish stocks on which research is being undertaken, and also the narrow continental shelf is not easily trawled. Thus it would be advisable to use corers or grabs instead of trawls to collect samples offshore of the East Coast due to the different sediment types. As the DEAT research vessels are located in Cape Town, it is too expensive to cruise up to the East Coast to collect invertebrate samples. Hence, the question of getting a research vessel into the region is still unanswered. An ROV would once again appear to be the best, and in the long run, a cheaper option to study this region, in terms of being able to sample the varied sediment

types and strong depth gradients. The African Coelacanth Ecosystem Programme (ACEP) programme have recently acquired an ROV and this could possibly be used in conjunction with offshore benthic invertebrate distribution surveys if the funding and ship time becomes available.

The effects of trawling on the benthic invertebrate fauna are not well established along the South African coast. Trawling in South Africa takes place to approximately 700 m depth along the West and South Coasts. Trawls used in the deep-sea are typically fitted with large trawl doors, which can weigh up to a ton each, and are largely unselective of the species caught (Davies *et al.,* 2007). Studies in other countries have shown that the damage to non-target epibenthic species, such as sponges, anemones and corals, is the most significant effect of trawling (Fosså *et al.,* 2002; Hall-Spencer *et al.,* 2002; Koslow *et al.,* 2001; Pitcher *et al.,* 2000; Roberts *et al.,* 2000). The long-term effects of the removal of these long-lived animals are for the most part unknown (Gage 2001) however, these species themselves provide habitat for parasites, attached internal symbionts and especially external symbionts (Grassle, 1991). Hence their removal would greatly affect the species diversity and richness of the communities in these trawling areas, and have a knock-on effect, as habitat removal will cause a decrease or even disappearance of the smaller species that are dependent on the long-lived animals.

When planning a network of offshore MPAs in South African waters the commercial fisheries and other deep sea industries, such as mining and oil exploration, need to be taken into account and economic impacts and livelihoods need to be considered. Sink *et al.* (2010) used the computer programme Marxan to determine areas to place MPA's and they utilized a 'cost metric equation' to determine the areas of high cost, i.e. these would be areas were fishing/trawling was very important and would therefore not be considered as MPA's, or at least not as complete no-take MPA's. The planning programme is still in progress, but benthic invertebrate community data have not been assessed as yet, and therefore the affect of trawling on the benthic invertebrates on the soft sediment environments that were sampled during my study will still be added to the planning programme.

The final recommendation is that offshore marine protected areas (MPA's) be placed offshore of the Namaqua National Park and the Tsitsikamma National Park (Figure 5.4) to conserve benthic invertebrate fauna and benthic ecosystems (Table 5.5). If the Tsitsikamma National Park were extended offshore it would conserve the Africana groups/communities 3, 6, 15 and 16. On the West Coast, the most important group/community to protect would be the Nansen group/community 2, the group/community with more than 15 % unique species. This is probably an important group/community, due to the fact that it lies on the continental shelf, and this is where other studies have shown that species richness increases (Weinberg, 1994; McClatchi *et al*., 1997; Labropoulou and Papaconstantinou, 2004). The Namaqua National Park would also conserve the Africana groups 2, 6, 7, 8, 12 and Nansen group 1, 2 and 5.

Table 5.5. The groups/communities found with unique species, not present in any of the other groups/communities found during the Nansen West Coast survey and the Africana South and West Coast surveys..

	Group/ Community	Percentage unique species (%)	Major contributing species
Nansen West Coast	Group 1	1	Mursia cristiata
	Group 2	15.5	Sympagurus dimorphus
Africana South and West Coast	Group 5	1.5	Solasteridae
	Group 6	1	Polychaeta sp. 6/Holothuroidea sp. 4
	Group 7	1	Spatangus capensis
	Group 10	1	Suberites sp.

The grid blocks used to depict the MPA's are the same size as those used by the commercial fishing industry (20x20 minute commercial reference grid cells) (Lombard *et al.,* 2004). The extension of the Namaqua National Park into a marine area is in fact being planned at the moment. This will incorporate eight groups/communities on the West Coast that have been identified by this study. Another four groups/communities could be added if the Tsitsikamma National Park could be extended offshore. The majority of groups/communities determined through this study will be conserved with the addition of only these two Parks offshore of South Africa. These two MPA's are chosen due to the fact that terrestrial Parks already exist along the coast in these areas and thereby costs will be saved by a seaward extension to the reserves, rather than creating entirely new conservation areas. Further research is, however, required as the groups/communities were only derived from three surveys in total and long term sampling is needed. More sampling also needs to be undertaken to determine what groups/communities are found offshore of the East Coast, and hence where the most appropriate area would be to place an offshore MPA in that region.

To determine the impact of climate change on the benthic environment, it is suggested that sampling of the benthic invertebrate bycatch continues over a number of seasons, so as to determine if there are large fluctuations in the environmental factors and hence changes in the distribution, abundance and biomass of benthic invertebrates offshore of the West and South Coasts of South Africa.

In conclusion, the offshore benthic environment of South African remains largely unknown, and the type of sampling undertaken for this study needs to continue so that patterns of the deep-sea benthos become clearer. Understanding the biodiversity of the deep-sea and the occurrence, distribution, biomass and biology of the benthic invertebrate species becomes essential when one needs to estimate the extent of human impact and climate change on the seafloor. It seems that photographic surveys undertaken with ROV's would be the best way to sample the deep-sea, however acquiring an ROV will probably exceed

the capacity of most research budgets. Hence, until this can be undertaken, surveys using trawls, or at least the same sampling methodology across the board, remain the most practical method for gathering quantitative comparable information regarding the benthic fauna.

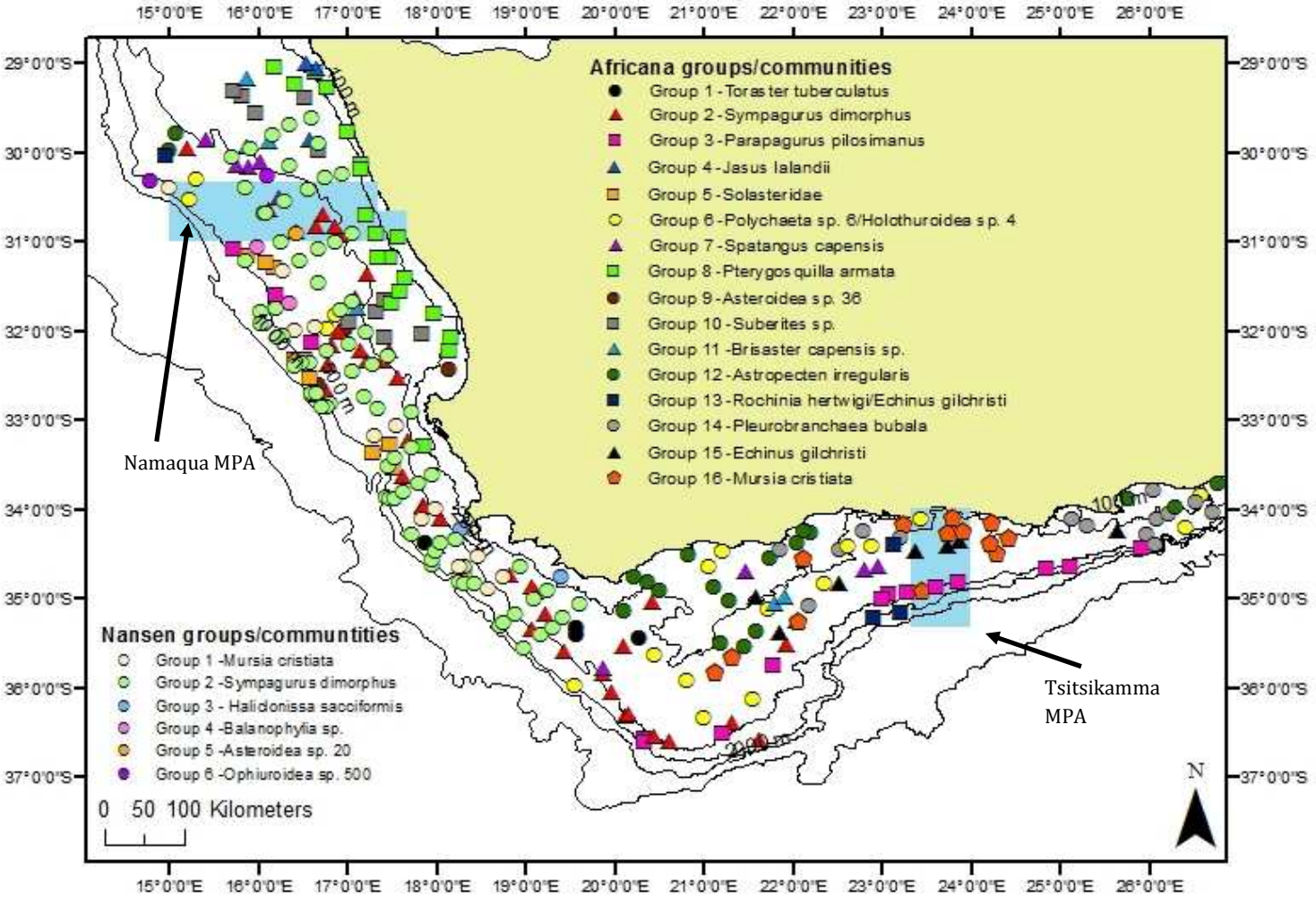

Figure 5.4. Map depicting the marine areas best suited to conserve the groups/communities found by this study offshore of the West and South Coasts of South Africa.

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